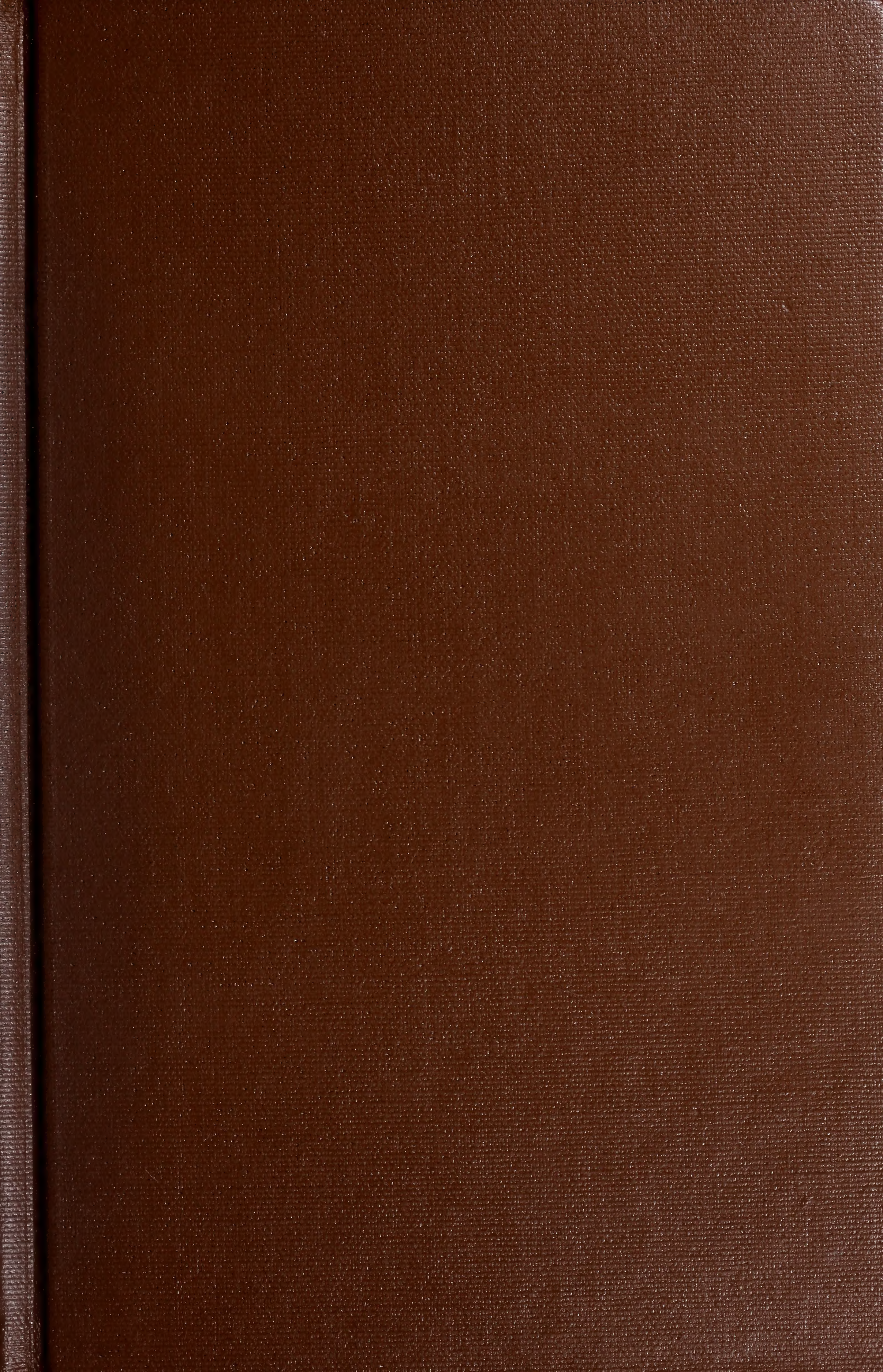



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Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Correlates of systematic differentiation between two closely related allopatric populations of the *Akodon boliviensis* group from NW Argentina (Rodentia: Cricetidae)

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Abstract

Studied external, epigenetic, and continuous morphological characters, karyotypes and allozymic genetic distances of *Akodon alterus* und *Akodon "tucumanensis"*. These forms are closely related deserving for some authors only subspecies status, but they are restricted to quite different biomes in the NW of Argentina. Cytogenetic results demonstrated chromosomal identity between them, as reflected by sharing the same 2n = 40, FN = 40 karyotype with an identical pattern of heterochromatin and a complete G-band arm-to-arm matching. Allozymic analysis revealed a low genetic distance between them, in agreement with previously reported D values for other *Akodon* species. *A. alterus* and *A. "tucumanensis"* can be differentiated by morphological characters and different habitat preferences. Previous reports suggested that adaptative divergence played a minor role in the cladogenesis of *Akodon* and that the main factor in its multifarious speciation may have been the stochastic and sudden fixation of chromosomal mutations eliciting reproductive isolation. *A. "tucumanensis"* and *A. alterus* may be an exception to this rule, or reflect strong habitat differentation in a single species complex. This example could be analyzed within the framework of a lack of correlation between organismic evolution and chromosomal and allozymic evolution.

Introduction

With about 43 living species and a fossil record tracing their origin back to the Pliocene, South American mice of the genus *Akodon* (sensu Reig, 1987, 1989; but see Spotorno 1986) are an interesting case of speedy and bountiful speciation. In view of their morphological resemblance and the frequency of several species packings in the same general biotopes, together with the wide range of chromosomal rearrangements and the high frequency of karyotypic species-specificity, it has been recently suggested that the main factor in *Akodon* multifarious speciation may have been the stochastic and sudden fixation of chromosomal mutations eliciting reproductive isolation. Under this process, ecological equivalence and morphological resemblance are to be expected, with selection acting mainly to tune up minor differentiation, but not being the main original agent of species differentiation (Reig 1989). Additionally, the overall speed of the process predicts small interspecific genetic differentiation, a prediction which has been widely corroborated (Apfelbaum and Reig 1989; Patton et al. 1989).

However, studies aiming to compare morphological, ecological, chromosomal and genetic-distances differences between pairs of closely related forms of *Akodon* supposedly involved in recent speciation, are lacking. These studies may be critical to further understanding the acting forces of speciation in these mice.

We have recently found that the most abundant species of mice in the high alpine steppe

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(3000 m) of the mountain valleys at "El Infiernillo" in the Aconquija range of Tucumán Province, was a small pale-coloured akodont, *Akodon alterus*, which has remained unnoticed so far at this location. As previously carried out by OLDFIELD THOMAS' collector EMILIO BUDIN and several other mammalogists, we collected in the subtropical forest and sugar cane plantations of the lowland environments in Tucumán province specimens of a small dark species of *Akodon* currently identified as *Akodon boliviensis tucumanensis*. This species is sympatric and syntopic with *A. puer* (= *A. caenosus*), *A. simulator*, and *A. illuteus*, all of which are clearly separated by their karyotypes, body size, or other minor morphological differences (BARQUEZ et al. 1980; LIASCOVICH et al. 1989). Routine karyotyping demonstrated that the high-grassland pale form is identical in its chromosomal complement to *A. b. tucumanensis*, which suggests a close relationship in spite of their strong ecological differentiation. In contrast with the general model referred to above, this suggests adaptive geographical speciation. We decided then to further study the relationships and degree of morphological, allozymic and chromosomal differentiation among these two forms.

Material and methods

Taxonomy and ecology

Akodon boliviensis, the type species of the genus *Akodon*, was described by MEYEN (1833) on specimens from Pichu Pichún, Arequipa Department, Perú. *Akodon tucumanensis* was described by ALLEN (1901) on specimens from San Miguel de Tucumán, 450 m, Tucumán Province, Argentina. CABRERA (1961) considered the Tucumanian form as a subspecies of *A. boliviensis* proposing the trinomen *A. b. tucumanensis*. Another related species, *A. spegazzini*, was described by THOMAS (1897) from lower Río Cachi, Salta Province, Argentina. Recently, MYERS et al. (1990) revised the taxonomy of several *Akodon* species from Perú, Bolivia, and the north of Argentina, which they placed together in a "*boliviensis* group", and includes *A. boliviensis, A. spegazzini, A. puer, A. subfuscus* and *A. juninensis*. They suggested that *tucumanensis* is a subspecies of *A. spegazzini*. We study here specimens collected near the type locality of *A. tucumanensis*. As we are not able to decide whether *A. tucumanensis* is a subspecies of *A. boliviensis* or of *A. spegazzini*, we will provisionally refer to our specimens as *A. "tucumanensis"*.

Akodon alterus was described by THOMAS (1991a) on specimens from Otro Cerro, at 3000 m, 45 km west of Chumbicha, in La Rioja Province, Argentina. He distinguished them from *A. spegazzini* by their drab brown colour instead of the buffy olive of the latter, and "by the absence of the strong yellowish or buffy suffusion in the fur". He also referred two specimens as *A. alterus* from Chumbicha, at 600 m, Catamarca Province, Argentina, one of which he had previously referred to *A. azarae* (THOMAS 1919b). He later (THOMAS 1920) described as the same species a series of 8 males and 17 females from La Invernada, at 3800 m and 3 males and 4 females from Potrerillo, at 1500 m, both localities near "Nevado de Famatina", in La Rioja Province. CABRERA (1961) considered *A. alterus* as a synonym of *A. b. tucumanensis*.

We captured 37 specimens (18 males and 19 females) of *A. "tucumanensis"* in August, 1986 and June, 1987 in Quebrada de Los Sosa, Tucumán Province, Argentina. Quebrada de Los Sosa is located approximately 25 km W of the city of San Miguel de Tucumán, on Route 307, at an elevation of 850 m. The area belongs to the Basal Subtropical Forest within the Provincia de Las Yungas (CABRERA 1976). Many epiphytes are present and the forest is largely evergreen. This area is characterized by *Phoebe porphyria* (laurel), *Cedrela lilloi* and *Cedrela angustifolia* (cedro), *Rapanea laetevirens* (palo San Antonio), *Tipuana tipu* (tipa), and *Tabebuia avellanedae* (lapacho) as the most conspicuous trees. Furthermore, there are shrubs, such as *Carica quercifolia* (higuera del monte) and climbing-plants, *Mitostigma latiflorum* and *Cynanchum trilobulatum* (MEYER 1963; CABRERA 1976). Although *A. "tucumanensis"* is the prevailing species in the trapping site (trapping success for this species was 18 % in 1986 and 23 % in 1987) we have also captured specimens of *A. simulator, A. illuteus, Oligoryzomys* sp., *Lutrolina crassicaudata* and *Thylamys* sp.

Additionally, at El Infiernillo, 79 km on Route 307, at an elevation of 3000 m, Tucumán Province, Argentina, we captured 24 specimens (12 males and 12 females) of a small pale akodont mouse identified as *A. alterus*. This locality is separated approximately 220 km from the type locality of *A. alterus* but it belongs to the same biome of high meadow steppe. El Infiernillo belongs to the Provincia Prepuneña (CABRERA 1976) characterized by the grasses *Stipa* (probably *S. saltensis*) and *Festuca* (probably *F. setifolia*), *Trichocereus pasacana* (cardón) covered by the epiphyte *Tillandsia*, and plants of the genus *Azorella, Adesmia*, and *Pycnophyllum*. The trapping success was 60 % in 1986 and 85 % in 1987. *A. alterus* was documented in a rodent guild in which we collected *Oligoryzomys flavescens*,

Phyllotis osilae, Ctenomys tuconax, and *Reithrodon auritus*. In the same locality DALBY (1974) reported the finding of the latter, together with *Andinomys edax* and *Calomys musculinus*. His reference to *A. andinus* and *Akodon* sp. may belong to *A. alterus*. We had previously collected *A. simulator* in the same locality but in a more rocky habitat (REIG unpubl.). Comparisons with the type and original specimens of *A. alterus* in the British Museum of Natural History demonstrated that specimens from "El Infiernillo" must be ascribed to this species.

In addition to the differences previously described in the flora of El Infiernillo and Quebrada de Los Sosa, the habitats of both localities are also remarkably different for most abiotic factors. Total rainfall measured at Quebrada de Los Sosa and El Infiernillo are 1432.8 mm/year and 422.8 mm/year, respectively. The rainfall is seasonally distributed with a peak in summer in both localities. However, precipitation exceeds 100 mm from November to March in Quebrada de Los Sosa, while this amount is achieved only in January in El Infiernillo. Moreover, there is a long dry season in El Infiernillo. The annual mean temperatures in Quebrada de Los Sosa and El Infiernillo are 15 °C and 10 °C respectively.

Morphology

Twenty three specimens of *A. alterus* and 27 of *A. "tucumanensis"* were analysed. Skulls were prepared for examination by the papain technique, modified from Luther (SEARLE 1954) further stained with alizarin red "S" (NOBACK and NOBACK 1944). An analysis of epigenetic characters was performed, following GRUNEBERG's (1952) definition and BERRY's (1963) and BERRY and SEARLE (1963) character-state descriptions for *Mus musculus*, and HEDGES' (1969) for *Apodemus sylvaticus* and *Apodemus flavicollis*. We followed Reig's (1977) nomenclature for enameled molar character-states. Bilateral traits were studied separately on either side. Some of the skulls were partly damaged and it was impossible to study all the characters. All determinations were made by the same observer (SB). We first analysed 45 discontinuous characters, but after preliminary analysis we eliminated some traits for obvious redundancy, strong correlation, and ambiguous or difficult recognition. Thus, we studied 35 characters which include the mandibular foramen, frontal wormian, fused frontals, emplacement of the posterior palatine foramen (right and left) and other 30 characters shown in Figures 1, 2 and 3. The MMD statistics modified by SJOVOLD (1973) was applied. Nine morphometric characters were also analysed, as detailed in Figure 1. Discriminant analysis was performed by means of STATGRAF statistical package.

Voucher specimens were deposited in the Museo Municipal de Ciencias Naturales "Lorenzo Scaglia", Mar del Plata, Argentina (MMP).

Cytogenetics

Twelve specimens of *A. alterus* and 26 of *A. tucumanensis* were analysed. Metaphase-chromosome preparations were obtained from bone marrow of animals injected with yeast one day before sacrifice, (LEE and ELDER 1980). Chromosomal spreads were stained with Giemsa or processed for G- and C-bands following SEABRIGHT (1971) and BARROS and PATTON (1985), respectively. Diploid number, fundamental number (FN), and chromosomal morphology for all specimens were determined. Fundamental number is the number of autosomal arms. Chromosomes were classified according to LEVAN et al. (1964). A modification of REIG and KIBLISKY's (1969) size proposal as a percentage of the female haploid set (FHS) was used classifying "large" those chromosomes $> 9\%$ FHS, "medium" those $> 5.5\%$ FHS, but $\leq 9\%$, "small" those $> 2\%$ FHS but $\leq 5.5\%$ FHS, and "minute" those $< 2\%$ FHS.

Allozymic distance

Tissues for electrophoresis and protein staining from 27 specimens of *A. alterus* and 31 of *A. "tucumanensis"* were prepared using the techniques employed by APFELBAUM and REIG (1989). Twenty eight presumptive loci were determined: Acid phosphatase (Acph), Aspartate aminotransferase (Aat-1, Aat-2), Esterase (Es-3, Es-4, Es-5), Fumarase (Fum-1, Fum-2), General Proteins (GP-1, GP-2), Glucose-6 Phosphate dehydrogenase (G-6pdh), Glycerophosphate dehydrogenase (Gpdh), Hemoglobine (Hb), Isocitrate dehydrogenase (Idh-1, Idh-2), Lactate dehydrogenase (Ldh-1, Ldh-2), Leucine aminopeptidase (Lap), Malate dehydrogenase (Mdh-1, Mdh-2), Malic enzyme (Me), Peptidase (Pep-1, Pep-2), Phosphoglucomutase (Pgm-1, Pgm-2, Pgm-3), Superoxide dismutase (Sd), and Xanthine dehydrogenase (Xdh). All differences in electrophoretic mobility were assumed to be of genetic origin and inherited in a Mendelian fashion. Alleles are designated alphabetically by their relative mobility, "a" represents the allele variant that migrates further anodally. Allozymic frequencies for each sample were determined from electrophoretic data and estimated by means of LEVENE's (1949) formula for small samples. Estimates of genic heterozygosity were obtained from the electromorphic genotypes by direct counts and averaged across loci for population estimates of individual variability (H), proportion of polymorphic loci per population (P), and average number of

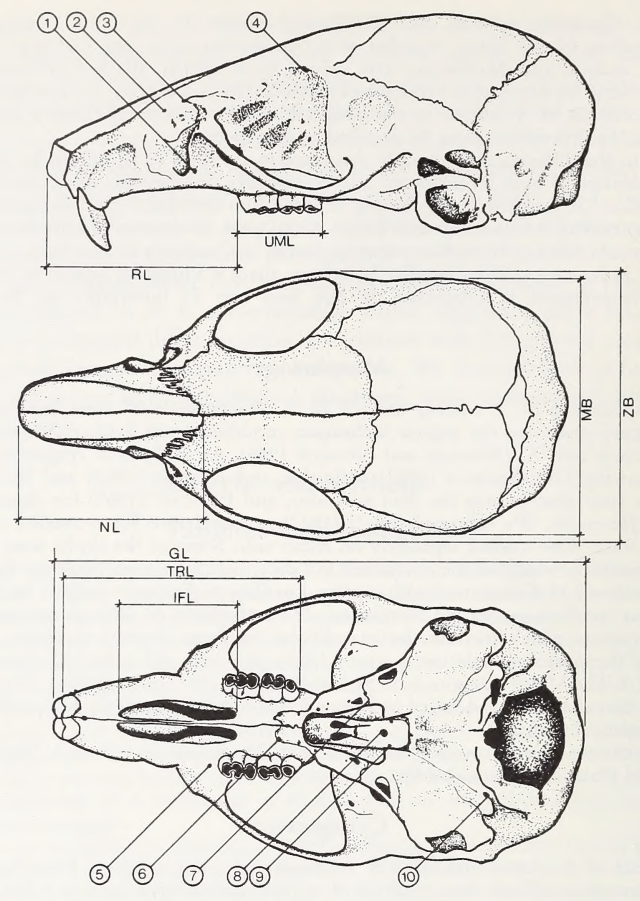


Fig. 1. Lateral (A), dorsal (B), and ventral views of skull of *A. "tucumanensis"*: 1-preorbital foramen I, 2-preorbital foramen II, 3-zygomatic plate foramen, 4-frontal foramen, 5-maxillary foramen, 6-posterior palatine foramen, 7-palatine-alisphenoid suture, 8-foramen sphenoidale medium, 9-ventrolateral sphenoidale foramen, 10-foramen hypoglossi, RL-rostrum length, UML-upper molar length, MB-mastoid breadth, ZB-zygomatic breadth, NL-nasal length, GL-greatest length, RTL-teeth row length, and IFL-incisive foramen length

alleles per locus (A). Genetic distance was estimated to measure the genetic divergence (Nei 1972) using the jackknife approach of Muller and Ayala (1982) as implemented in the program of Sattler and Hilburn (1985).

Results

Morphology

The percentage occurrence of individual non-metrical characters examined in both samples are given in Tables 1 and 2. The value of the mean measure of divergence is $4.405276 \times 10-2$ and its standard deviation $1.055756 \times 10-2$. The MMD is significant at (approximately) the 0.025 probability level when it is greater than twice its standard deviation (Sjovold 1973; Nevez 1984).

The following characters show strong differences in frequency between the two forms or are exclusive in one of them (Tables 1, 2), thus affording the main variables to

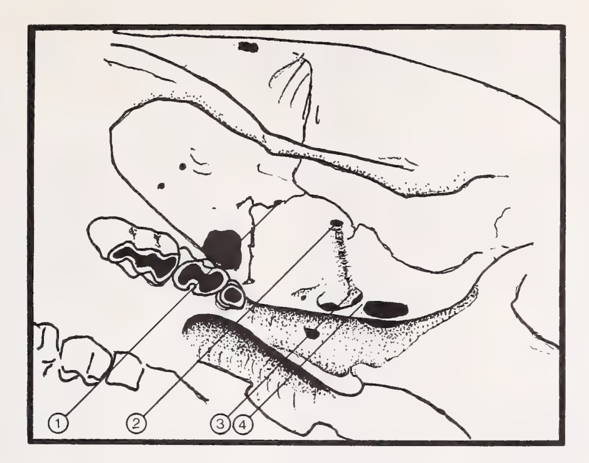


Fig. 2. Detail of the ventro-lateral view of skull of *A. "tucumanensis"*: 1-orbito-alisphenoid foramen, 2-upper buccino masticatory foramen, 34-buccino masticatory foramen, and 4-alisphenoid strut

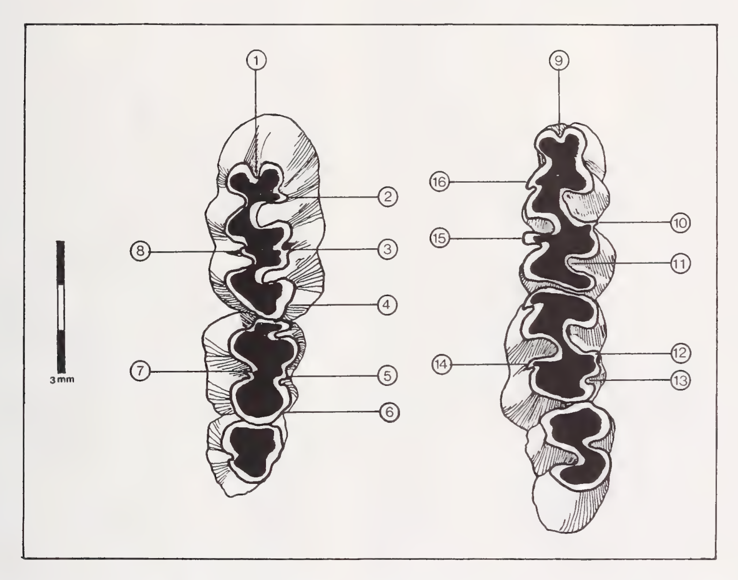


Fig. 3. Left upper molar row (A) and left lower molar row (B) of a female of *A. alterus* from El Infiernillo, Tucumán Province, Argentina: 1-anteromedian flexus of M1; 2-anteroloph-parastyle of M1; 3-mesostyle-mesoloph of M1; 4-posteroloph-posterostyle of M1; 5-mesostyle-mesoloph of M2; 6-posteroloph-posterostyle of M2; 7-enterostyle of M2; 8-enterostyle of M1; 9-anteromedian flexid of m1; 10-mesostylid-mesolophid of m1; 11-posterolophid-posterostylid of m1; 12-mesostylid-mesolophid of m2; 13-posterolophid-posterostylid of m2; 14-ectostylid of m2; 15-ectostylid of m1; and 16-protostylid of m1

distinguish the two forms: posterior palatine foramen (triple), frontal foramen (absent or present), foramen sphenoidale medium (absent and double), mandibular foramen (triple), mesostyle-mesoloph M1 (absent or present), enterostyle M1 (moderate or well-developed), anteromedian flexid (absent or present), posteroloph-posterostyle M1 (moderate or well-developed), posterolophid-posterostylid of m1 (absent and moderatly developed), posteroloph-posterostyle of M2 (moderate or well-developed).

Table 1. **Percentage occurrence of individual non-metrical skull characters of *A. alterus (A.a.)* and *A. "tucumanensis" (A.t.)***

Character	% *A.a.*	% *A.t.*	Character	% *A.a.*	% *A.t.*
Zygomatic plate foramen ra	9.5	10.5	For esp. ventrolateral lp	0.0	10.0
Zygomatic plate foramen r1	42.8	57.9	Foramen hypoglossi r1	65.0	79.0
Zygomatic plate foramen rm	47.6	31.6	Foramen hypoglossi r2	35.0	21.1
Zygomatic plate foramen 1a	0.0	10.0	Foramen hypoglossi l1	55.0	73.7
Zygomatic plate foramen l1	61.9	60.0	Foramen hypoglossi l2	45.0	26.3
Zygomatic plate foramen lm	38.1	30.0	Alisphenoid canal ra	100.0	90.0
Preorbital foramen I r1	85.7	75.0	Alisphenoid canal rp	0.0	10.0
Preorbital foramen I r2	14.3	25.0	Alisphenoid canal la	90.5	80.0
Preorbital foramen I l1	85.7	95.0	Alisphenoid canal lp	9.5	20.0
Preorbital foramen I l2	14.3	5.0	For. orbito-alisph. x' ra	71.4	75.0
Preorbital foramen II ra	14.3	35.0	For. orbito-alisph. x' rp	28.6	25.0
Preorbital foramen II rp	85.7	65.0	For. orbito-alisph. x' la	76.2	80.0
Preorbital foramen II la	33.3	52.7	For. orbito-alisph. x' lp	23.8	20.0
Preorbital foramen II lp	66.7	47.3	For. buccino-mast. sup. ra	23.8	30.0
Frontal foramen ra	0.0	5.0	For. buccino-mast. sup. rp	76.2	70.0
Frontal foramen r1	33.3	45.0	For. buccino-mast. sup. la	28.6	25.0
Frontal foramen r2	52.4	30.0	For. buccino-mast. sup. lp	71.4	75.0
Frontal foramen rm	14.3	20.0	For bucc. mast. ra	0.0	10.0
Frontal foramen la	0.0	10.0	For bucc. mast. r2	80.6	65.0
Frontal foramen l1	28.6	50.0	For bucc. mast. rm	19.4	25.0
Frontal foramen l2	47.6	35.0	For bucc. mast. la	9.5	20.0
Frontal foramen lm	23.8	5.0	For bucc. mast. l2	61.9	70.0
Maxillary foramen ra	4.8	15.0	For bucc. mast. lm	28.6	10.0
Maxillary foramen r1	47.6	50.0	Alisphenoid strut ra	0.0	10.0
Maxillary foramen rm	47.6	35.0	Alisphenoid strut rp	100.0	90.0
Maxillary foramen la	4.8	5.0	Alisphenoid strut la	9.5	10.0
Maxillary foramen l1	47.6	50.0	Alisphenoid strut rp	90.5	90.0
Maxillary foramen lm	47.6	45.0	Frontal wormian a	71.4	90.0
Posterior palatine foramen r1 (ppf)	80.9	85.0	Frontal wormian p	28.6	10.0
Posterior palatine foramen r2 (ppf)	19.1	10.0	Fused frontals a	19.1	15.0
Posterior palatine foramen rm (ppf)	0.0	5.0	Fused frontals p	80.9	85.0
Posterior palatine foramen l1 (ppf)	85.7	85.0	Emplacement of the ppf rm	23.8	15.8
Posterior palatine foramen l2 (ppf)	14.3	15.0	Emplacement of the ppf rs	19.0	26.3
Palatine-alisphenoid suture rn	55.0	80.0	Emplacement of the ppf rp	57.1	57.9
Palatine-alisphenoid suture rt	45.0	20.0	Emplacement of the ppf lm	42.9	10.5
Palatine-alisphenoid suture ln	50.0	60.0	Emplacement of the ppf ls	14.3	31.6
Palatine-alisphenoid suture lt	50.0	40.0	Emplacement of the ppf lp	42.8	57.9
Foramen sphenoidale medium a	0.0	10.0	Mandibular foramen r1	85.7	90.0
Foramen sphenoidale medium 1	100.0	75.0	Mandibular foramen r2	4.8	10.0
Foramen sphenoidale medium 2	0.0	15.0	Mandibular foramen r3	9.6	0.0
For esp. ventrolateral ra	95.0	95.0	Mandibular foramen l1	80.9	90.0
For esp. ventrolateral rp	5.0	5.0	Mandibular foramen l2	14.3	10.0
For esp. ventrolateral la	100.0	90.0	Mandibular foramen l3	4.8	0.0

r = right, l = left, a = absent, p = present, 1 = simple, 2 = double, m = multiple, n = anterior, t = transverse.

Regarding the morphometric analysis, highly significant differences were found between both groups (DF = 9, X2 = 25.29, at level = 0.003). Analysis of the discriminant function indicates that the most important variables in the differentiation were in order of precedence lower molar length (LML), rostrum length (RL), and length of incisive foramen (IFL) (see Table 3).

Cytogenetics

A. "tucumanensis" and *A. alterus* have an identical 2n = 40, FN = 40 karyotype (Fig. 4). Pairs 1 to 18 are constituted by telocentric chromosomes, while pair 19 is made of

Table 2. **Percentage occurrence of individual non-metrical molar characters of *A. alterus (A.a.)* and *A. "tucumanensis" (A.t.)***

Character	% *A.a.*	% *A.t.*	Character	% *A.a.*	% *A.t.*
Anteromedian flexus M1 ra	9.5	11.8	Antermedian flexid m1 rm	4.8	23.5
Anteromedian flexus M1 rm	23.8	41.2	Antermedian flexid m1 rd	95.2	76.5
Anteromedian flexus M1 rd	66.6	47.0	Antermedian flexid m1 la	0.0	5.9
Anteromedian flexus M1 la	4.9	5.9	Antermedian flexid m1 lm	4.8	23.5
Anteromedian flexus M1 lm	28.7	52.9	Antermedian flexid m1 ld	95.2	70.6
Anteromedian flexus M1 ld	66.5	41.2	Protostylid m1 ra	4.8	11.8
Mesostyle-Mesolph M1 ra	0.0	5.9	Protostylid m1 rm	14.3	23.5
Mesostyle-Mesolph M1 rm	76.2	29.4	Protostylid m1 rd	80.9	64.7
Mesostyle-Mesolph M1 rd	23.8	64.7	Protostylid m1 lm	14.3	29.4
Mesostyle-Mesolph M1 la	0.0	5.9	Protostylid m1 ld	85.7	70.6
Mesostyle-Mesolph M1 lm	57.1	23.6	Mesostylid-Mesolophid m1 ra	23.8	29.4
Mesostyle-Mesolph M1 ld	42.9	70.6	Mesostylid-Mesolophid m1 rm	71.4	52.9
Enterostyle M1 ra	47.6	2.4	Mesostylid-Mesolophid m1 rd	4.8	17.6
Enterostyle M1 rm	52.4	5.9	Mesostylid-Mesolophid m1 la	14.3	47.1
Enterostyle M1 rd	0.0	11.7	Mesostylid-Mesolophid m1 lm	85.7	47.1
Enterostyle M1 la	52.4	76.4	Mesostylid-Mesolophid m1 ld	0.0	5.9
Enterostyle M1 lm	47.6	11.9	Ectostylyd m1 ra	4.8	5.9
Enterostyle M1 ld	0.0	11.8	Ectostylyd m1 rm	71.4	58.8
Anteroloph-Parastyle M1 rm	42.9	17.7	Ectostylyd m1 rd	23.8	35.3
Anteroloph-Parastyle M1 rd	57.1	82.3	Ectostylyd m1 la	4.8	11.8
Anteroloph-Parastyle M1 lm	38.1	17.7	Ectostylyd m1 lm	61.9	58.8
Anteroloph-Parastyle M1 id	61.9	82.3	Ectostylyd m1 ld	33.3	29.4
Posteroloph-Posterostyle M1 ra	38.1	82.3	Mesostylid-Mesolophid m2 ra	66.7	70.6
Posteroloph-Posterostyle M1 rm	61.9	11.8	Mesostylid-Mesolophid m2 rm	33.3	29.4
Posteroloph-Posterostyle M1 rd	0.0	5.9	Mesostylid-Mesolophid m2 la	57.1	64.7
Posteroloph-Posterostyle M1 la	28.6	94.1	Mesostylid-Mesolophid m2 lm	42.9	35.3
Posteroloph-Posterostyle M1 lm	71.4	5.9	Ectostylid m2 ra	47.6	76.5
Mesostyle-Mesoloph M2 ra	9.5	5.0	Ectostylid m2 rm	52.4	23.5
Mesostyle-Mesoloph M2 rm	85.7	58.8	Ectostylid m2 la	47.6	76.5
Mesostyle-Mesoloph M2 rd	4.8	11.9	Ectostylid m2 lm	52.4	17.7
Mesostyle-Mesoloph M2 la	9.5	23.5	Ectostylid m2 ld	0.0	5.9
Mesostyle-Mesoloph M2 lm	85.7	64.7	Posterolophid-Posterostylid m1 ra	19.1	0.0
Mesostyle-Mesoloph M2 ld	4.8	11.8	Posterolophid-Posterostylid m1 rm	0.0	5.9
Enterostyle M2 ra	95.2	88.2	Posterolophid-Posterostylid m1 rd	80.9	94.1
Enterostyle M2 rm	4.8	11.8	Posterolophid-Posterostylid m1 la	19.1	0.0
Enterostyle M2 la	100.0	88.2	Posterolophid-Posterostylid m1 lm	0.0	5.9
Enterostyle M2 lm	0.0	11.8	Posterolophid-Posterostylid m1 ld	80.9	94.1
Posteroloph-Posterostyle M2 ra	61.9	94.1	Posterolophid-Posterostylid m2 ra	4.8	23.5
Posteroloph-Posterostyle M2 rm	23.8	0.0	Posterolophid-Posterostylid m2 rm	52.4	41.2
Posteroloph-Posterostyle M2 rd	14.3	5.9	Posterolophid-Posterostylid m2 rd	42.8	35.3
Posteroloph-Posterostyle M2 la	47.6	88.2	Posterolophid-Posterostylid m2 la	4.8	17.7
Posteroloph-Posterostyle M2 lm	38.1	5.9	Posterolophid-Posterostylid m2 lm	42.8	47.1
Posteroloph-Posterostyle M2 ld	14.3	5.9	Posterolophid-Posterostylid m2 ld	52.4	35.3

e = right, l = left, a = absent, m = moderate, d = development.

metacentric minute chromosomes. Pair 1 is large, easy to identify by size from the remaining autosomal pairs. Pairs 2 to 6 are medium-sized and pairs 7 to 18 are small autosomes gradually decreasing in size. The X is subtelocentric and the Y is submetacentric, representing 8.40 % and 3.21 % of the complement, respectively. A polymorphism of the sexual pair has been found in females of both species. Two types of females were found: females with XX sex chromosomes, and females with XXd sex chromosomes being the Xd an X-chromosome with a gross deletion in its long arm. In the present report over a total of 19 *A. "tucumanensis"* females analyzed, 9 were XX and 10 were XXd and over a total of 12 *A. alterus* females, 8 were XX and 4 were XXd. The Xd represents a 3.23 % of

Table 3. **Measurements (mm) of *A. alterus* (A.a.) and *A. "tucumanensis" (A.t.)* holotypes, and samples of El Infiernillo and Quebrada de Los Sosa**

	A.a. X	*A.a.* SD	*A.a.* Type ♂ BMNH 19.2.7.44	*A.t.* X	*A.t.* SD	*A.t.* Type ♀ BMNH 0.7.9.13
Greatest length	23.9	0.8	–	23.6	0.9	–
Rostrum length	8.2	0.0	–	8.6	0.0	–
Nasal length	8.2	0.0	–	8.5	0.1	–
Zygomatic breadth	12.5	0.0	–	12.6	0.4	–
Mastoid breadth	11.4	0.0	–	11.3	0.0	11.7
Teeth row length	10.5	0.0	–	10.7	0.0	–
Incisive foramen length	6.0	0.0	–	6.1	0.0	–
Upper molar length	4.5	0.0	4.0	4.4	0.0	4.2
Lower molar length	4.6	0.0	4.4	4.4	0.0	4.2

X = mean; SD = standard deviation.

the complement in *A. "tucumanensis"*, and a 3.93 % in *A. alterus*. It is of interest to notice that in spite of the X polymorphism the sex ratio was nearly 1:1 in the samples of both species.

C-bands (Fig. 4) showed that constitutive heterochromatin is located in the whole short arm of the X, the Xd-chromosome and the Y, in both species. Figure 5 shows a total G-band correspondence of chromosome arms between *A. "tucumanensis"* and *A. alterus.*

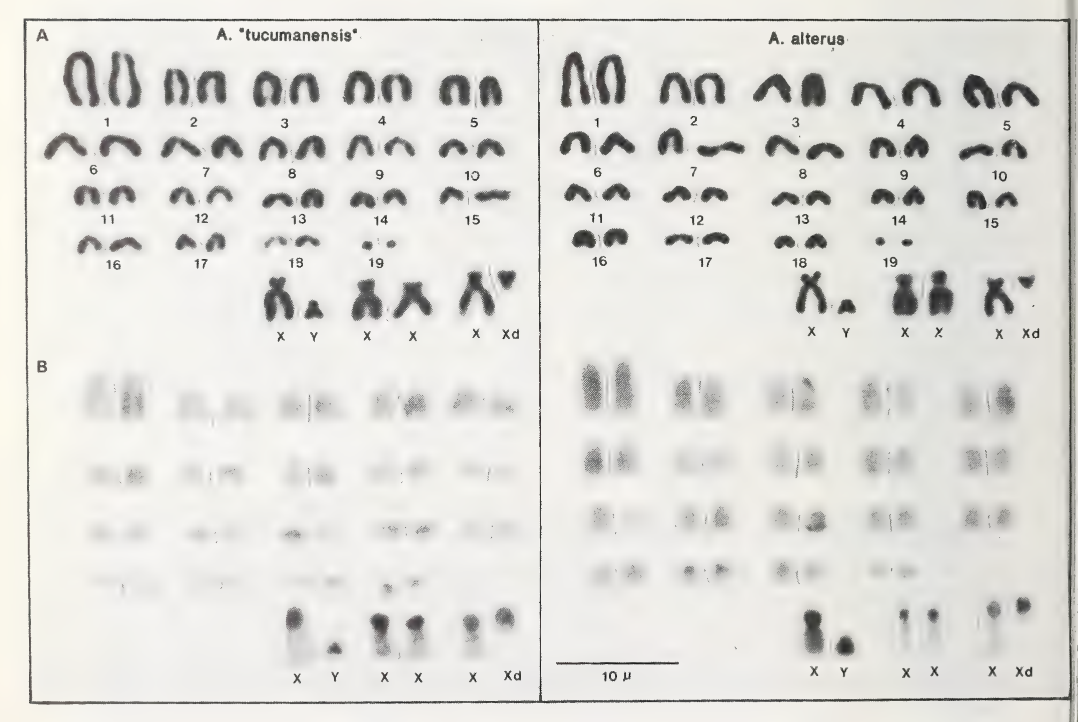


Fig. 4. A. "tucumanensis" (left) and *A. alterus* (right) Giemsa-stained karyotypes (A), and C-bands (B)



Fig. 5. G-banding pattern comparison between *A. "tucumanensis"* and *A. alterus*. Each pair is composed of one autosome of *A. "tucumanensis"* (left) and one of *A. alterus* (right)

Allozymic distance

Of the 28 loci examined electrophoretically, 20 (71.4 %) were monomorphic and fixed for the same allele in the two samples. The remaining 8 loci (28.6 %) were polymorphic in one of the two analysed species. The value of (A) was 1.082 in *A. alterus* and 1.111 in *A. "tucumanensis"*, (H) was 7.6 % in *A. alterus* and 10 % in *A. "tucumanensis"*, and (P) was 21.42 % in *A. alterus* and 25 % in *A. "tucumanensis"*. Estimates of genetic distance (D) values between the two forms showed an average value of D = 0.0280.

Discussion

There is ample evidence that organismic evolution is not always accompanied by chromosomal and allozymic changes. Against the conclusion of Wilson et al. (1975) several taxa show high chromosomal differences among synmorphic species, while others show a high degree of organismal differentiation within karyotypic invariance (Reig 1984). In rodents in which chromosomal variability is the rule, a correlation between the rate of chromosomal change and speciation rate has been suggested (Wilson et al. 1975; Bush et al. 1977; Aguilera 1980; Imai 1983). Based on the correlation between high species-diversity and high karyotypic heterogeneity patterns, Reig (1989) suggested that chromosomal repatterning could be a prime causative factor of speciogenesis in the akodontine and in other groups of rodents.

Modern theoretical developments suggest that phenotypic evolution is the result of changes in developmental programs strongly mediated by the evolution of regulatory genes with direct influence on epigenesis (Arthur 1984). Changes in structural genes, whatever their adaptative or neutral character, may be inconsequential to evolution. Although

chromosomal rearrangements may affect regulatory patterns, some of them may also be inconsequential to organismal evolution the underlying reorganization of the DNA may or may not have phenotypic effects (Rose and Doolittle 1983).

Among Sigmodontinae rodents, *Akodon* (sensu Reig 1987, 1989) shows a high degree of chromosomal variability, their karyotypes ranging from 2n = 14 (in *A. "arviculoides"*, Yonenaga (1972) to 2n = 52 (in *A. longipilis,* Spotorno and Fernandez 1976). The exceptions are a few species which share the same 2n = 52 karyotype (Gallardo 1982; Rodriguez et al. 1983; Liascovich et al. 1989). However, these species have been recently separated as members of the genus *Abrothrix* (Spotorno 1986; Barrantes et al. 1991), in which case, *Akodon* is limited to a group of species showing a high degree of chromosomal heterogeneity. The high level of interspecific chromosomal variability of *Akodon* is not matched by a sharp morphological differentiation. The subtlety of morphological limits among *Akodon* species is a permanent difficulty to taxonomists and hampered progress in assessing the status of their species.

The mean genetic divergence among *Akodon* species is very small indeed, and it is only matched among rodents by a few other exceptional cases. Interspecific genetic distances in mammals are regularly greater than D = 0.2 (see Apfelbaum and Reig 1989). It is interesting to note that small genetic differentiation is negatively correlated with a high rate of chromosomal rearrangements in this genus, suggesting that karyotypic repatterning played a primary role in eliciting species richness, and that genetic differentiation mostly reflects divergence times. The finding of low levels of genetic distance and of morphological similarity together with the relatively eurytopic and generalized habits in *Akodon* species allow us to speculate that adaptative divergence played a minor role in its speciose cladogenesis. Our results of allozymic analysis revealed a low genetic distance of D = 0.028 between *A. "tucumanensis"* and *A. alterus*. This figure agrees with previously reported values for other *Akodon* species. For example, genetic distance between pairwise comparison with *A. longipilis/A. xanthorhinus* (D = 0.022) *A. iniscatus/A. neocenus* was D = 0.021 and *A. "tucumanensis"/A. molinae* was D = 0.030. However, slightly high D values were found among *A. "tucumanensis"/A. puer* (D = 0.122), *A. "tucumanensis", A. albiventer/A. kempi* (D = 0.190), and *A. azarae/A. cursor* (D = 0.154) (Apfelbaum and Reig 1989; Patton et al. 1989; Barrantes et al. 1991).

Cytogenetic results have shown chromosomal conservatism between *A. "tucumanensis"* and *A. alterus* as reflected by a complete G-band correspondence. Moreover, both species share the same chromosomal polymorphism in the X-chromosome. This kind of chromosomal variability was also found in other species of the genus which belong to the group of species of around 40 or more reduced diploid numbers (*A. azarae*, Bianchi and Contreras 1967; Lizarralde et al. 1982; *A. puer*, Kajon et al. 1984; Vitullo et al. 1986; *A. neocenus* (cited as *A. varius*), Bianchi et al. 1971; *A. cursor*, Yonenaga-Yassuda 1979). The meaning of the X polymorphism in *Akodon azarae* has been discussed by Bianchi et al. (1989) and Solari et al. (1989).

However, these two forms can be differentiated by their external (coloration and body size), epigenetic, and continuous morphological characters. Additionally, both forms inhabit quite different ecological habitats in allopatric distribution; *A. alterus* inhabits the high mountain steppes, whereas *A. "tucumanensis"* inhabits the humid lower mountain forests.

The morphological differentiation between our samples of *A. alterus* and *A. "tucumanensis"* is indeed comparable to that found in different local populations of small mammals inhabiting different habitats. This would suggest that Cabrera was not wrong in placing *alterus* as a junior synonym of *boliviensis* , or, that both are mere subspecies of the same species. The small genetic distance, and the lack of chromosomal difference between the two forms would reinforce this view. However, as there is a strong ecological and a less marked morphological differentiation between them, and as several *Akodon* species share

similar karyotypes and very small allozyme differentiation, we believe that any conclusion on the taxonomic status of the two forms is untimely. A definite solution must wait further sampling in intermediate localities and the investigation of isolation mechanisms.

If the morphologic and ecological differences are enough to consider the two forms as full species, our results are in agreement with the pattern observed in the 2n = 52 species now referred to as *Abrothrix* , which are only distinguished morphologically (see SPOTORNO 1986; SPOTORNO et al. 1990).

It may be significant that we have failed to obtain laboratory hybrids between *A. alterus* and *A. "tucumanensis"* because the behavior of the couples was strongly aggressive. Nevertheless, since we also observed a high level of intraspecific aggressiness in mating trials of *A. "tucumanensis"*, this result may not be considered conclusive.

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Zusammenfassung

Korrelate von systematischer Differenzierung bei zwei nahe verwandten allopatrischen Populationen von Akodon aus der Boliviensis-Gruppe des Nordwestens von Argentinien (Rodentia, Cricetidae)

A. alterus und *A. „tucumanensis"* wurden bezüglich ihrer äußerlichen, epigenetischen und kontinuierlichen morphologischen Merkmale, der Karyotypen und der allozymischen, genetischen Abstände untersucht. Diese beiden Arten scheinen eng miteinander verwandt zu sein, leben aber in zwei verschiedenen Biotopen im Nordwesten von Argentinien. Die cytogenetischen Ergebnisse zeigen eine große Übereinstimmung zwischen beiden Arten: eine gleiche diploide Zahl der Chromosomen (2n = 40), eine gleiche fundamentale Zahl (NF = 40), eine gleiche Heterochromatin-Verteilung und eine vollständige Homologie der G-Bandenmuster. Die allozymische Analyse ergab ferner eine geringe genetische Distanz zwischen beiden Arten. Dieses stimmt mit Werten bei Gegenüberstellung von anderen überein. *A. alterus* und *A. „tucumanensis"* können aber durch ihre morphologischen Merkmale und die verschiedenen Habitate voneinander unterschieden werden. Frühere Untersuchungen weisen darauf hin, daß die adaptive Divergenz eine geringe Rolle in der Kladogenese von *Akodon* gespielt hat, und daß sich die große artliche Vielfalt auf eine stochastische und schnelle Fixierung von chromosomischen Mutationen zurückführen läßt, welche zur reproduktiven Isolation geführt haben. Wir fanden heraus, daß *A. „tucumanensis"* und *A. alterus* eine Ausnahme von dieser Regel darstellen. Dieses Beispiel kann im Kontext mit der Abwesenheit von Korrelationen zwischen organismischer Evolution und chromosomischer, allozymischer Evolution analysiert werden.

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Correlative genital tract morphology and plasma progesterone levels during the ovarian cycle in Corn mice (*Calomys musculinus*)[1]

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Abstract

Described the correlation between genital tract morphology and plasma progesterone in laboratory-reared corn mice (*Calomys musculinus*). Morphological traits of the ovary, uterus and vagina were used to define stages of the estrous cycle and of some anovulatory states. These findings were correlated with changes in the vaginal smear and in plasma progesterone (as measured by radioimmunoassay). Estrous cyclicity and ovulation occurred in females caged without males. Plasma progesterone during the estrous cycle showed both a periovulatory and a postovulatory peak. Changes in the vaginal smear correlated poorly with ovarian changes, except the formation of new corpora lutea, that correlated with a sudden disappearance of cornified cells from the smear. The most frequent cycle length was 5 days. Finally, two histologically distinct anovulatory conditions were found associated with basal progesterone levels. The ovarian cycle of this species is provisionally classified as type III of Conaway (1971), (spontaneous ovulation, induced luteal phase).

Introduction

Calomys musculinus, the corn mouse, is probably the most widespread species of field mice in Argentina. It is found from near Esquel (43° South latitude) to the tropical boundaries with Bolivia and Paraguay, and from the Andes (2230 meters altitude at Maymará, the type locality, province of Jujuy) to sea level in the province of Buenos Aires. In the humid and temperate Pampa's grasslands this species acts as reservoir of Junín virus, the etiologic agent of Argentine hemorrhagic fever (Sabattini et al. 1977; Weissenbacher and Damonte 1983).

Reproductive mechanisms of the corn mouse may also be interesting in the context of the evolution of muroid rodents, because South American cricetids are a monophyletic group (Subfamily Sigmodontinae; Reig 1980) that probably differentiated from North American cricetids in the early Miocene (Reig 1982), some 22 million years ago. The murids (laboratory rats and mice included), whose reproductive biology is, by far, the best known, only emerged as a distinct group some 15 million years ago (Walker 1964).

The corn mouse breeds mainly in the spring and summer, but can also reproduce all year round, particularly when winters are not too severe (Mills et al. 1992). In the laboratory, it has a gestation period of 21 days, a mean litter size of 4.4 to 7.6 young and a postpartum estrus (de Villafañe 1981; Hodara et al. 1984).

The present paper describe the ovarian, uterine and vaginal changes occurring during the estrous cycle of this species, and in two distinct anovulatory conditions that were found. Also, plasma progesterone levels were measured in both cycling and anovulating females, and in males.

1 This work is dedicated to Professor John W. Everett on his 85. birthday.

Material and methods

Animals

Colony bred animals were studied after 7–8 weeks of age (fertile copulations can occur as early as the 4th week; de Villafañe 1981). The colony originated in 1983 from wild mice captured in two localities (La Pega and Ñacuñán) of the province of Mendoza. Animals from the two localities have been bred as separate lines ever since. However, there were no apparent differences between lines, and all the groups presented here were composed of females from both. The females were kept in groups of 4–8, in 12 × 20 × 30 cm cages, without males within the cage, under 14 h light/10 h dark, and at 24 °C, and they had free access to a balanced diet and water.

Vaginal smears

Vaginal smears were obtained daily (for periods of 14 to 54 days) in most females, by vaginal lavage with a small pipette. The smears were dried in an oven, fixed in ethyl ether and absolute ethanol (1:1), and stained by the method of Papanicolaou (1954), with minor modifications. In some cases, the material for smearing was not taken, because the vaginal orifice was extremely narrow or closed.

Sacrifices and plasma sampling for progesterone determination

All sacrifices were made in the evening. One hundred and sixty one females were sacrificed under ether to establish the correlation between ovarian histology and the other features of the genital tract. Vaginal smears were taken from 114 of these females, before sacrificing them at selected stages of the vaginal smear. The remaining 47, from which smears were not taken, were sacrificed on random days. The uterine horns were inspected for the presence of intraluminal fluid, before the genital tract was removed. The ovaries and uteri were trimmed of surrounding tissues, and weighed. Ovaries and vaginas were fixed in Stieve's fluid and embedded in paraffin. Tissue sections were stained with haematoxylin and eosin. The ovaries were sectioned serially.

Additionally, 80 females and 10 males were sacrificed by decapitation and trunk blood was collected in heparinized tubes for progesterone determinations. Females were sacrificed at selected stages of the vaginal smear, and were autopsied as described in the above paragraph. Plasma was separated by centrifugation and kept frozen until the day the radioimmunoassay was performed as previously described (Bussmann and Deis 1979; Castro-Vazquez and Carreno 1981).

Ovarian follicles

The largest follicle with no signs of atresia, was classified as either type 5b, 6, 7 or 8, according to Pedersen and Peters (1968): 5b-largest preantral follicles; 6-growing follicles with antral lacunae; 7-growing follicles with a single antral cavity and a well-defined cumulus oophorus; and 8-Graafian follicles with a definite cumulus stalk.

Corpora lutea (CL)

They were classified in four classes, that seem to represent the sequence of corpus luteum (CL) formation and regression, and that were defined as follows: Ia – approximately spherical CLs, with or without a central cavity (the collapsed 'channel' through which the ovum was apparently shed, could still be recognized in CLs without a cavity); the cavities were sometimes filled with blood cells and/or fibroblasts; the luteal cells were large and lightly acidophilic, with clear nuclei and distinct nucleoli; frequently both hollow and solid CLs were seen in the same animal and, therefore, were considered as a single class; Ib – spherical CLs with no cavities or 'channels', and with luteal cells as in Ia; II – CLs that were frequently deformed by adjacent structures and showed an increased proportion of fibroblasts; most luteal cells were smaller than in Ia or Ib, and their nuclei were usually smaller and/or darker, and had absent or unconspicuous nucleoli; and III – small and distorted CLs with much connective tissue surrounding groups of small luteal cells with lightly stained cytoplasm.

Statistics

Multi-group comparisons between means (ovarian and uterine weights) were made by analysis of variance, using the Tukey test for post-hoc analysis. Multi-group comparisons of the incidence of vaginal cornification, uterine fluid or old corpora lutea were made with the chi-square test (2-tailed)

for k-samples. Post-hoc analysis between two groups was made either with the chi-square test or with the Fisher's exact probability test, as recommended in Siegel (1956). Significance level was fixed at $P < 0.05$.

Results

I – Ovarian stages and their associated uterine and vaginal changes

Females that exhibited ovarian signs of recent or impending ovulation, were classified as proestrous, estrous, metestrous or diestrous, according to criteria defined below. However, near 50 % of females were in one of two anovulatory conditions. The main features of these ovulatory and anovulatory classes were as follows (see also Tables 1 and 2).

Table 1. **Age and body weight, and histological features of the ovary, in female Corn mice in different ovarian stages**

Ovarian stage	Number of cases	Age, days (a)	Body weight, g (b)	Type of the largest follicle	Type of the most recent corpus luteum
Proestrus	14	163 ± 11	19.3 ± 0.8	7	none, II or III
Estrus	21	130 ± 15	17.1 ± 0.8	8, or recently ruptured ones	none, II or III
Metestrus	26	163 ± 10	18.8 ± 0.7	5b–6	Ia
Diestrus	23	163 ± 12	19.3 ± 0.8	5b–6	Ib or II
Atretic cycles	13	140 ± 17	16.6 ± 0.7	5b–6	none, II or III
Anestrus	64	146 ± 5	16.8 ± 0.4	5b–6	none or III

(a) Mean ± S.E.M. No significant differences (Tukey test); (b) Mean ± S.E.M. 'Anestrus' differed significantly from all groups except 'Estrus' and 'Atretic cycles'. 'Atretic cycles' differed significantly from 'Proestrus' and 'Diestrus' ($p < 0.05$; Tukey test).

Table 2. **Other ovarian, uterine and vaginal features in female Corn mice in different ovarian stages (a)**

Ovarian stage	Ovarian weight (b) mg	Old corpora lutea (c) %	Uterine weight (b) mg	Distended uteri (d) %	Open vaginas (e) %	Cornified vaginas (f) %
Proestrus	4.9 ± 0.4	85.7	60.4 ± 11.3	42.9	71.4	58.3 (12)
Estrus	4.5 ± 0.3	85.7	56.5 ± 4.6	90.5	100.0	94.7 (19)
Metestrus	4.4 ± 0.2	65.4	50.0 ± 5.2	19.2	96.0 (25)	0 (24)
Diestrus	4.5 ± 0.3	73.9	43.9 ± 2.5	13.0	87.0	0
Atretic cycles	3.0 ± 0.4	69.2	26.9 ± 4.7	15.4	81.8 (11)	30.8
Anestrus	2.2 ± 0.1	10.9	11.9 ± 0.6	0	37.5	19.3 (57)

(a) Values which are not percentages are expressed as mean ± S.E.M. Unless otherwise indicated in parentheses, the number of cases in each group is the same as in Table 1; (b) 'Anestrus' and 'Atretic cycles' differed significantly between them and from all other groups ($P < 0.05$; Tukey test); (c) % of animals with type II and/or type III corpora lutea. Only 'Anestrus' differed significantly from all other groups ($P < 0.05$; Chi-square test); (d) 'Anestrus' and 'Estrus' differed significantly between them and from all other groups ($P < 0.05$; Chi-square test, followed by Chi-square or Fisher's test as 'post hoc' analysis; (e) 'Anestrus' differed significantly from all other groups. Also, 'Proestrus' differed significantly from 'Estrus' and 'Metestrus' ($P < 0.05$; Chi-square test, followed by Chi-square or Fisher's test as 'post hoc' analysis; (f) 'Anestrus' differed significantly from all groups except 'Atretic cycles'. Also, 'Atretic cycles' differed significantly from 'Estrus', 'Metestrus' and 'Diestrus', and 'Proestrus' differed significantly from 'Metestrus' and 'Diestrus' ($P < 0.05$; Chi-square test, followed by Chi-square or Fisher's test as 'post hoc' analysis).

1 – 'Proestrus'

Ovaries contained type 7 follicles, but no recent CLs (types Ia and Ib); type II and/or type III CLs were present in most cases. The uterus was dilated with fluid, and/or the vaginal epithelium was cornified, in approximately 50 % of these females; however, the vagina was closed in 4 out of 14 animals.

2 – 'Estrus'

The ovaries had large Graafian follicles (type 8) or recently ruptured, unluteinized ones. A cornified vaginal epithelium, a uterus dilated with fluid, and one or two sets of regressing CLs (type II and/or III) were found in most cases.

3 – 'Metestrus'

Ovaries contained newly formed CLs (type Ia); in 2 cases these contained trapped ova. Most ovaries also had one or two older generations of CLs (types II and/or III). The largest growing follicles varied from stages 5b to 7. The vaginal epithelium had always lost the cornified layer. The uterus was sometimes dilated with fluid.

4 – 'Diestrus'

Ovaries in which the largest follicle was type 5b or 6, and the most recent CLs were either type Ib (i.e., similar to Ia, but with no cavities nor 'channels') or type II. One or two older generations of CLs were also common. The vaginal epithelium was never cornified and sometimes was atrophic. The uterus was sometimes dilated with fluid.

5 – 'Anestrus'

The largest follicle was a type 5b (occasionally, type 6), and follicles in varying degrees of atresia were typical. The CLs were absent, or old (type III). The uteri were small and thread-like, with no intraluminal fluid. Vagina histology was very variable: the most common was a low squamous epithelium, infiltrated with leucocytes. When the vaginal orifice was closed (62.5 % of cases), the epithelium was atrophic and frequently covered with a layer of columnar mucous cells. In some cases with open vaginas, however, the epithelium was cornified. This can be correlated with the occasional days of cornification that interrupt the leucocytic smear pattern of these animals.

6 – 'Atretic cycles'

The largest growing follicles were type 5b or 6. CLs were absent or regressing (type II or III). In addition, there was a set of large atretic follicles, that appeared to have interrupted their growth simultaneously, contrasting with the asynchronous stages of atresia commonly found in anestrous ovaries. The incidence of type II and/or type III CLs (indicative of ovulation in the preceding cycle) did not differ from that in females undergoing ovulatory cycles, but was significantly higher than in anestrous females. The uteri were also significantly heavier than those of anestrous females, and were sometimes dilated with fluid. Vagina histology was as variable as in anestrus, and cornified epithelia were also found.

II – Patterns of changes in the vaginal smear

The vaginal smear of females that were not in anestrus at sacrifice (Fig. 1A) was characterized by the cyclic occurrence of waves of nucleated and cornified cells (modal length: 2 days), that were often accompanied by enlarged and swollen vaginal orifice. The onset of these epithelial waves was indicated by a decrease in the proportion of leucocytes and the appearance of cornified cells, sometimes preceded by small, nucleated epithelial cells (intensely stained with light green). Leucocytes disappeared from the smear only rarely, although they were definitely reduced in number during the epithelial waves. At the end of these waves, cornified cells disappeared, and a stage dominated by large, nucleated epithelial cells, sometimes preceded the ensuing series of predominantly leucocytic smears. Mucous smears occurred frequently during the leucocytic intervals between epithelial waves. The vaginal orifice narrowed during these intervals and sometimes closed completely.

Despite following the vaginal cycle before sacrificing animals, the vaginal smear frequently did not correlate closely with the status of the ovary at autopsy. For instance, proestrous ovaries sometimes coexisted with closed vaginas, or smears that varied from fully leucocytic to fully cornified ones, and fully cornified smears, typical of estrus, were

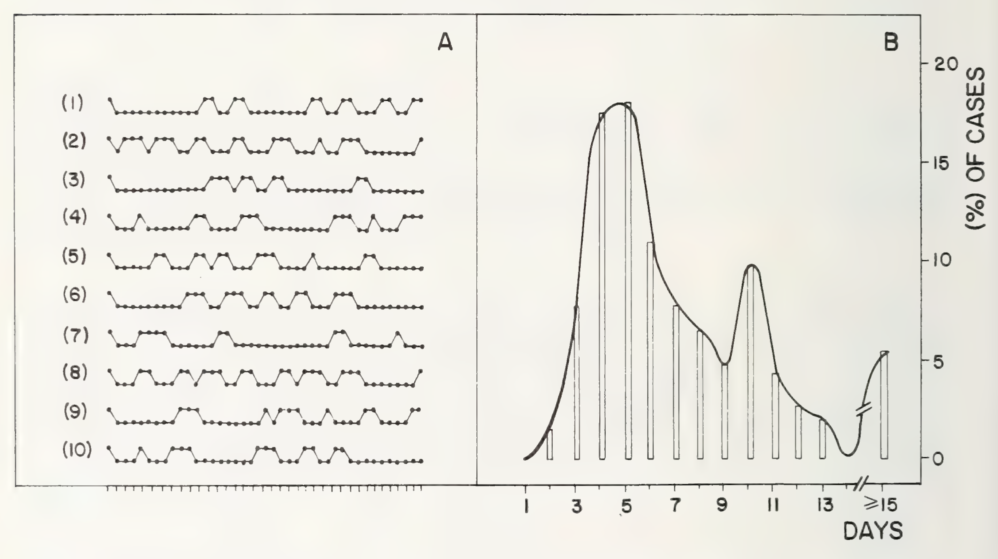


Fig. 1. Sequence of vaginal cycles in 10 selected cases that were observed during forty days (panel A); the upper points of each line on panel A indicate the days dominated by epithelial cells (either nucleated or cornified ones), while the lower points indicate the days of the diestrous intervals. Panel B shows a histogram of duration of vaginal cycles in 57 females that were not found in anestrus at sacrifice

sometimes found in anestrous animals. The disappearance of the cornified layer at metestrus, however, was clearly and reproducible reflected in the smear and was the only vaginal event that could be reliably correlated with a change in the ovary.

A histogram of cycle lengths of females that were not in anestrus at sacrifice is shown in Figure 1B. The cycles were considered to begin when cornified cells disappeared from the smear, and to continue until the next disappearance of cornified cells: 182 cycles were recorded, from 57 females. Cycles length was very variable, with a mode of 5 days and a second frequency peak at 10 days.

On the other hand, females found in anestrus at sacrifice, were characterized by periods

of persistent leucocytic smears and/or closed vaginal orifices. In half of these, also, there was at least one episode of smears dominated by nucleated and/or cornified cells. However, these periods of epithelial cells were shorter (modal length: 1 day) than in non-anestrous females.

III – Incidence of the different phases

The frequency of the different ovarian stages was determined in 47 females that were not smeared, and were sacrificed on random days. Anestrus was frequent (38.3 %), and the "atretic cycle" was infrequent (8.5 %). Proestrus, estrus and metestrus showed about the same incidence as the atretic cycle (10.0, 8.5 and 10.6 %, respectively), while diestrus was about twice as frequent (23.4 %). Then, if we consider that cyclic animals showed a modal cycle length of 5 days, we can estimate the duration of proestrus, estrus and metestrus as one day each, and the duration of diestrus as two days.

Table 3. **Plasma progesterone concentration (nmol/l; mean ± S.E.M.) in female Corn mice in different ovarian stages, and in males**

	Number of cases	Plasma progesterone (a)
Proestrus	8	20.0 ± 2.9
Estrus	10	49.9 ± 8.9
Metestrus	15	19.7 ± 1.9
Diestrus, type Ib	9	40.1 ± 3.2
Diestrus, type II	11	21.0 ± 2.9
Atretic cycles	5	12.4 ± 1.6
Anestrus	21	16.5 ± 1.3
Males	10	17.2 ± 4.1

(a) Either 'Estrus' or 'Diestrus, type Ib' differed significantly from all other groups ($P < 0.05$; Tukey test). Other differences were not significant

IV – Plasma progesterone levels in the different ovarian states and in males

Plasma progesterone differed significantly ($P < 0.05$; Tukey test) in diestrous females whether their most recent CLs were type Ib or II. It was higher in mice bearing type Ib CLs, which were usually found (8 out of 9 cases) on the third day of leucocytic smears, i.e., approximately on the second day of diestrous (Table 3). Progesterone levels in type Ib diestrus were also higher ($P < 0.05$ or better; Tukey test) than in any other group except estrus. Conversely, plasma progesterone during estrus was also significantly higher ($P < 0.01$; Tukey test) than in any other group except type Ib diestrus. Males, and those females in anestrus, atretic cycles, proestrus, and metestrus had basal progesterone levels, and did not differ significantly between them nor with type II diestrus.

Discussion

The vaginal smear pattern of cyclic female corn mice is difficult to interpret if compared with the common laboratory species, partly because of the lack of a definite indication of proestrus. Indeed, the corn mouse does not show the surface layer of swollen cells that occurs at proestrus in the rat and other mammals (e.g. Long and Evans 1922), and that brings about the massive shedding of proestrous rounded cells in those species. Another complicating factor may be the contamination of smears with cells from preceding stages that may be retained in the double cervicovaginal folds that are typical of the corn mouse (Castro-Vazquez et al. 1987).

It is then important to conclude that nothing can be said about the ovarian status of a living female, as in field studies, either from the vaginal smear or from the appearance of the external vaginal orifice on the day of capture. In the laboratory, however, where vaginal smears can be studied during subsequent days, total cycle length can be estimated as the distance between two disappearances of cornified cells, since the occurrence of newly formed CLs (type Ia) was reliably associated with that vaginal event. Under these

conditions, the length of the cycle most frequently observed was 5 days, although somewhat longer cycles were also rather frequent, probably indicating the occurrence of short anestrous periods between the ovulatory cycles.

Short cycles as those described in the corn mouse have not been found outside the Superfamily Muroidea, but have been also described in many Muridae and Cricetidae, both from the Old World and from North and South America (Asdell 1964; Justines and Johnson 1970; Conaway 1954; Dewsbury et al. 1977), which suggests that this may be an early acquisition within this Superfamily. This short cycle has been always observed in association with spontaneous ovulation, and with an induced luteal phase (type III cycle in the classification of Conaway 1971), and appears typical of short life-span, high reproduction prey species. It seems that the mechanism of ovulation in the corn mouse is basically spontaneous, since ovarian evidence of past or impending ovulation was observed in about 60 % of females caged without males. We have not studied, however (and there are no reports, either) if it is possible to induce luteal activation by coital or cervicovaginal stimulation in the corn mouse. Therefore, we can only provisionally classify the corn mouse as bearing a type III cycle. A prolongation of luteal function after genital stimulation has been reported in some North American cricetids (Dewsbury and Estep 1975; Kenney et al. 1977), which are phylogenetically rather close to the South American ones.

Plasma progesterone in the corn mouse attains maximum levels during estrus and, after a nadir during metestrus, it peaks again in type Ib diestrus. A pattern of progesterone secretion that includes both a preovulatory (proestrous) and a postovulatory (diestrous) peak has been reported in many muroid rodents, including the laboratory rat (Butcher et al. 1974; Smith et al. 1975). It should be noted, however, that what we have designated here as 'estrus' is equivalent to what was called 'proestrus' in those studies. We preferred to designate this stage as 'estrus' in the corn mouse, since ovulation had already occurred in 4 out of 21 'estrous' animals that were sacrificed in the evening, and since ovulation only occurs about 10 hours later in the rat (Everett et al. 1949), i.e., in the early hours of the following day. However, both the estrous and the diestrous peaks of progesterone secretion are remarkably lower in the corn mouse than in the corresponding stages in the rat. The low level of circulating progesterone at estrus in the corn mouse may be correlated with the persistence of uterine fluid during metestrus and diestrus that occurs in some subjects, since progesterone secretion during the rat proestrus seems responsible for the rapid loss of uterine fluid that occurs in that species (Barnea et al. 1968). Anovulating female corn mice, as well as cycling females in stages other than estrus and type Ib diestrus, had low progesterone levels similar to those found in males. The occurrence of basal progesterone levels in late diestrus (type II) indicates that the function of the corpora lutea formed at ovulation is ephemeral, and further suggests that some form of luteal activation (induced luteal phase) should exist to render implantation possible.

The high incidence of anestrus in laboratory-reared corn mice may be explained, in principle, as an effect of (1) some dietary defficiency (for instance, 6-methoxybenzoxazolinone: Berger et al. 1981; Sanders et al. 1981; Schadler et al. 1988); (2) grouping (which may be act either through a pheromonal effect: Champlin 1977; or through establishing social ranks within the group: Bujalska 1973), and (3) prevention of male exposure (Montoro et al. 1987). No effort was made here to determining the cause of anestrus in our laboratory conditions. It is clear, however, that the high incidence of anestrus is an effect of captivity, since we found (Mills et al. 1992) that all feral adult females are reproductively active when captured during the breeding season.

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Zusammenfassung

Beziehungen zwischen Genitaltraktmorphologie und Plasmaprogesteronspiegel während des ovariellen Zyklus von Maismäusen (Calomys musculinus)

Beschrieben wird die Beziehung zwischen der Morphologie des Genitaltrakts und dem Progesteronspiegel im Plasma der Maismaus (*Calomys musculinus*). Morphologische Charakteristika des Ovars, des Uterus und der Vagina wurden zur Definition der Zyklusphasen und einiger anovulatorischer Zustände benutzt. Die Befunde wurden mit Veränderungen in Vaginalabstrichen in Beziehung gebracht sowie mit der Progesteronkonzentration im Plasma (gemessen mit Hilfe eines Radioimmunoassay). Bei Weibchen, die ohne Männchen gehalten wurden, traten Östrus und Ovulation zyklisch auf. Sowohl während wie auch nach der Ovulation zeigte die Progesteronkonzentration im Plasma Spitzenwerte. Veränderungen in den Vaginalabstrichen zeigten nur geringe Beziehungen zu Veränderungen im Ovar. Die Ausbildung frischer Gelbkörper war allerdings mit dem plötzlichen Verschwinden von Zellen des Stratum corneum aus dem Abstrich verbunden. In der Mehrzahl der Fälle betrug die Länge des Zyklus fünf Tage.

Der Ovarialzyklus der untersuchten Art wird in Anlehnung an Conaway (1971) vorläufig dem Typ III zugeordnet, welcher durch spontanen Eisprung und induzierte Lutealphase charakterisiert ist.

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New data on the burrowing behaviour of *Microtus* (*Pitymys*) *duodecimcostatus*

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Abstract

Described the burrowing behaviour of *Pitymys duodecimcostatus* in captivity. The digging patterns have been found to be different from those reported in earlier papers. Nine different behaviour patterns were recorded, five of them directly linked to the burrowing activity and the other being unrelated. The burrowing sequence was studied with respect to the five patterns directly related with the burrowing behaviour. Some differences between males and females were shown in the activities more or less related to digging. The main conclusion is that *Pitymys duodecimcostatus* uses the incisors as a digging tool in hard substrata, showing a behaviour similar to that of *Arvicola terrestris.* This behaviour seems to depend on the hardness of the excavated soil.

Introduction

Subterranean mammals have been classified by several authors according to the way they dig into the soil, i.e., their morphological adaptations and their digging behaviour. For instance, Agrawal (1967) distinguishes two kinds of fossorial rodents according to skull and forelegs morphological features, while Dubost (1968a, b) distinguishes three kinds of fossorial mammals: those using only or mainly the forelegs, those using the incisors, and those using teeth and forelegs.

More recently, Gasc et al. (1985) have proposed another classification which deals not only with the digging elements, but also with the burrowing modes. They consider two wide groups according to the parts of the body utilized: those using the forelegs (two subgroups, *Pitymys* and *Eremitalpa*) and those using the teeth (also two subgroups, *Arvicola terrestris* and *Spalax*). According to this classification, *Pitymys duodecimcostatus* would belong to the first group, but there is one difficulty: the Mediterranean vole does not show any modification of the forelegs for digging. This lack of specialization in the forelegs led Casinos et al. (1983) to postulate only a behavioural adaptation in *Pitymys duodecimcostatus,* without morphological changes. We have undertaken a study of the digging behaviour patterns in *Pitymys duodecimcostatus,* an attempt to add new data to those supplied by Casinos et al. (1983).

Material and methods

Observations were made on four adult females and three adult males of *Pitymys duodecimcostatus* caught in the Aisa valley at an altitude of 1680 m, not far from Jaca, in the Spanish Pyrenees. The animals were kept in individual glass boxes. Light followed the normal cycle and temperature was maintained between 10° and 20 °C. Within the boxes there was enough loose soil to allow digging, and also fibrous material for nest building. Food in surplus (mainly peanuts and carrots) was supplied.

Sixteen observations were made for each animal except one, a female, for which there were only thirteen observations possible. Each observation lasted for five minutes, and the different activities and their durations were noted. The observations were done in an experimental enclosure, a glass-walled box of 51 × 72 × 4 cm containing well-packed moist earth (2.3 kg/cm of compressive

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strength). The box was joined by a 10 cm long pipe to another transparent plastic box of 10 × 31 × 16 cm, where the animal transported the earth away from the former box. Later, observations were made in soft, unpacked soil (compressive strength 0.35 kg/cm, i.e., about seven times less than normal soil formerly used) on three adult females and two adult males. The observations were recorded by hand, vocally and videotape.

Nine different behavioural patterns were recorded, five of them directly linked to the burrowing activity, the other being unrelated behaviours. The same patterns were found in both sexes. Behaviour units lasted for different amounts of time, and were recorded as such, not by uniform time units. Sampling method was, therefore, a sequence record with repetitions excluded and with durations of each sequence added (SLATER 1978). The behavioural units were the following:

Digging (D): recorded whenever the animal tore out the earth by means of bites. The incisors played the main role, and the forelegs were used mainly to push the loose earth below the abdomen. Both forelegs worked independent by, the body being supported, during the biting phase, by the two hindlegs and by the non-workingforeleg. From time to time, when the amount of earth below the body was high, the animal threw the earth backwards with the hindlegs, in two or three kicks, and during this phase the body was supported on the forelegs. During the biting act (B) the forelegs were used for earth accumulation (A) and throwing away the earth with the hindlegs (H). Burrowing is, thus, a composite three-part behaviour.

Turning (T): recorded when the animal stopped to burrow and turned around by a lateral tumble, going then to the outside box.
Head pushing (Hp): recorded when the animal pushed the earth outwards, from the beginning of the tunnel. The head was used like a bulldozer blade during this activity.

Entrance kicking (Ek): when the animal was in the small plastic box but near the tunnel entrance, and kicked away the earth with the hindlegs before entering again into the burrow.

Tunnel kicking (Tk): the animal entered the tunnel, stopped from time to time, accumulated some earth with his forelegs, and kicked the accumulated earth backwards with the hindlegs. This movement was quite fast, and happened several times between the entrance and the arrival at the digging front.

Grooming (G): this included the common patterns of cleaning the face, the ears and the paws, followed by a regular washing of the body, which finished with the tail. Often it also included scratching the sides with a hindleg, which was also cleaned afterwards.
The other behavioural patterns found are: Feeding (F), Resting (R) and Sniffing (S).

Sequence analysis has been carried out following a first-order Markov model (FAGEN and YOUNG 1978). Statistical methods included are the Kolmogorov test for two samples, chi-square test and G test.

Results

Description of burrowing sequence

Burrowing sequence was studied with the first five types of acts, the other having a very low frequency. The sequence was independently established for males and for females, because there were significant differences in the frequency of acts between both sexes on the Markov model (G test level of significance: $p < 0.0001$). The analysis was repeated with only the three burrowing acts (B, A and H) together with the preceding and following acts, with similar results (G test significance level of sex differences: $p < 0.0001$). Sequences were later changed into probabilities (Fig. 1).

Within the burrowing sequence, biting (B) was followed by accumulation (A) with a high probability (0.98 for males, 0.93 for females). Accumulation (A) was then followed by biting (B) more often than by kicking (H) (0.62 for both sexes). After H, the probability of B was also larger than that of other acts, e.g., going outside the tunnel (T = 0.74 for males, 0.61 for females). On average, each burrowing sequence was made up of several repetitions; a low unit was made of three B and two A, while a higher order unit was made of two low-order units separated by one H. The mean number of repetitions for each digging act is shown in Figure 2. Also observations were made on the digging activity of the species in soft, unpacked soil. These show that the animal does not bite (B) at all, but only accumulates (A) and kicks (H) the earth (Fig. 2). There were significant differences between the acts in soft and hard soils (G test level of significance: $p < 0.0001$).

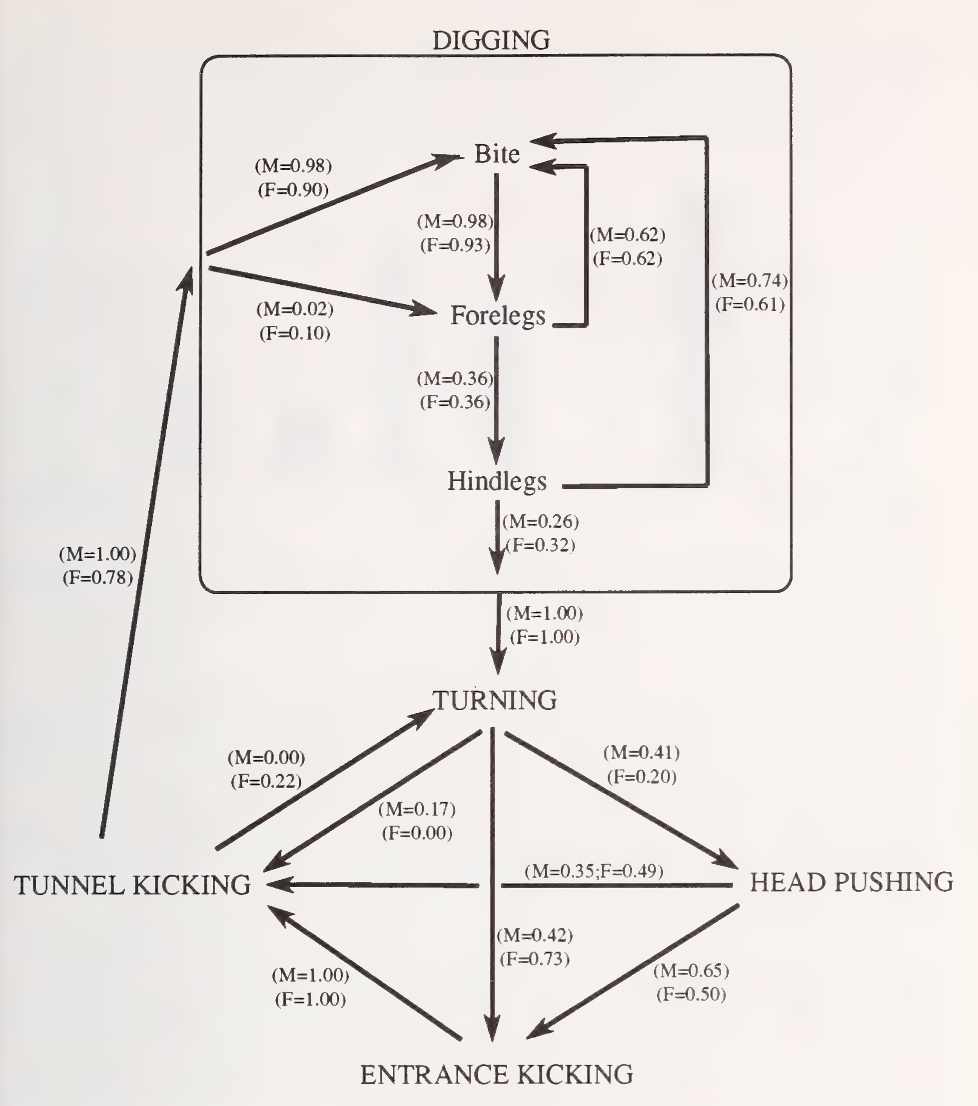


Fig. 1. Burrowing sequence and probabilities of each digging act of *Pitymys duodecimcostatus*. Within the box the set of acts is shown specifically belonging to digging activity. (M = males, F = females)

With respect to the more general sequence, with non digging acts included, the probability of the whole of B being followed by T is 1 in both sexes. T is sometimes followed by Hp, Ek or Tk. In the males, Ek or Hp have a similar probability, while among the females Ek has a higher probability of occurrence. Hp can precede Ek or Tk, with a similar probability in females and a higher probability for the sequence Hp-EK among males. Tk precedes B with a very high probability in both sexes, and within the burrowing sequence, the probability of beginning with biting (B) behaviour is very high, 0.98 for males and 0.90 for females.

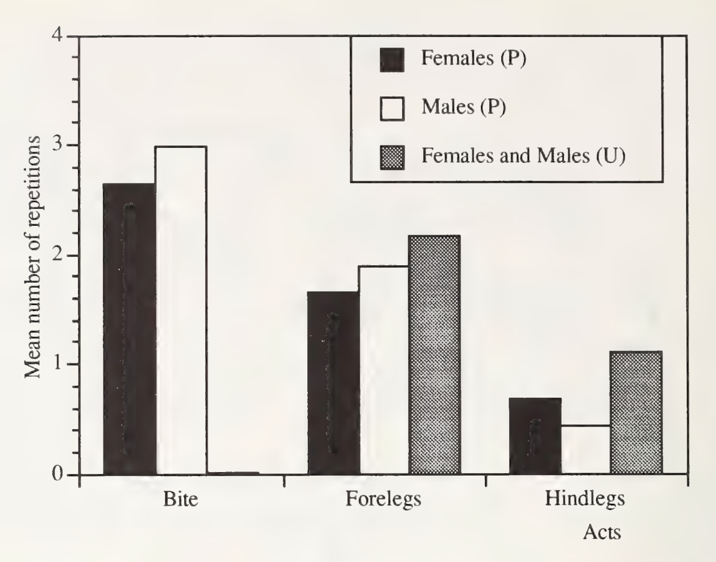


Fig. 2. Mean number of repetitions in each digging sequence, of the acts linked to burrowing behaviour. (P: observation on packed soil; U: observation on unpacked and soft soil)

Duration of sequences

The mean duration of each behaviour in seconds and the corresponding frequence are listed in the Table for both sexes. Some behaviours, such as feeding (F), last for a considerable time, but they are not frequent, and hence their total time is low. Other behaviour, such as digging (D), lasts long and is quite frequent, allowing much time for observation; e.g., total observation time of digging was over 70 min for the males and over 2 hours for females. On the other hand, the shorter behaviour was Ek, with a mean duration of 2.9 seconds in the males and 2.5 seconds in the females. The remaining acts were of intermediate duration.

There is some difference between males and females in the mean duration of each behaviour. When these differences are significant this is indicated in Table 1. The table also shows the percentage of time spent by each sex on each type of behaviour. A significant difference of the total time spent for each behaviour has also been shown (G test level of

Mean duration of each act in seconds for both sexes and percentage of total time spent in each kind of burrowing behaviour for both sexes

Acts	Mean duration				Percentage of time	
	male	(n)	female	(n)	male	female
Digging	16.0	(265)	14.1	(562)	33	41
Turning	7.1	(377)	3.9	(574)**	20	13
Head pushing	6.5	(136)	4.1	(98)	7	2
Ent. kicking	2.9	(262)	2.5	(521)	6	7
Tun. kicking	7.0	(394)	7.2	(656)	21	26
Grooming	8.6	(68)	7.6	(107)	4	4
Feeding	13.0	(9)	16.5	(13)	1	1
Resting	8.4	(54)	2.7	(71)*	3	1
Sniffing	6.0	(84)	3.5	(161)	4	3

* p = 0.01, ** p = 0.003 (Kolmogorov-Smirnov test).

significance: $p < 0.001$). Both males and females spent the main part of their time with digging (D = 43 % females and 32.7 % males), followed by the time spent on driving the earth out of the tunnel (Tk = 26.5 % females and 21.2 % males). The behaviours with the greatest difference between sexes were resting (R), and turning in the tunnel (T).

Discussion

With reference to the description and Figure 1 (which depicts this sequence) we can see that *Microtus* (*Pitymys*) *duodecimcostatus* uses mainly the mouth for burrowing, the forelegs to accumulate soil and the hindlegs to kick the earth away. This agrees with the conclusions of AGRAWAL (1967) for *Pitymys sikimensis,* but does not agree with the conclusions of CASINOS et al. (1983). According to these authors, *P. duodecimcostatus* uses its legs for burrowing, and GASC et al. (1985) included this species within the group of hand-diggers, and even names this group as *'Pitymys system'*.

It is possible thus to understand the lack of morphological adaptations for digging at the forelegs of this vole, because it uses the teeth, not the front feet, as does *Pitymys sikimensis.* AGRAWAL (1967) stated that the latter species uses its incisors to burrow and that skull and teeth morphology seem to be highly modified to fossorial activity. Moreover, MATHIAS (1990) found a strong proodontism both in *P. lusitanicus* and in *P. duodecimcostatus,* which is taken to be an adaptation to fossorial life.

Thus, the only remaining problem is the misconception by CASINOS et al. (1983) as to the burrowing method of the Mediterranean vole. The observations made by CASINOS et al. (1983) and by GASC et al. (1985) appear to be quite reliable. Therefore, the best way of explaining the discrepancy between their and our results is to suppose differences in the procedures of observation. The most evident of these is the soil supplied to the animals: the soil we used was well-packed, moist earth, while that of the former authors was loose peat; due to the need of using a substratum transparent to X rays required for radiocinematography. The burrowing behaviour of *P. duodecimcostatus* changes with the consistency of the available substratum.,Thus, in our observations the normal sequence was: -B-B-B-A-A-H-B-B-B-A-A-H-B-B-B-, but in different substrata the number of repetitions of each act and the general pattern could be modified, with the number of bites larger in hard soils and lower or null in soft soils.

The main conclusion is that *Pitymys duodecimcostatus* uses the incisors as a digging tool in hard substrates, showing a behaviour similar to that of *Arvicola terrestris,* according to the observations of AIROLDI et al. (1976) and LAVILLE (1989). In this case the species should be included in the group called "bite and tear system of *Arvicola terrestris*" by GASC et al. (1985).

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Zusammenfassung

Neue Angaben über das Verhalten von Microtus (Pitymys) duodecimcostatus beim Graben

Bei in Gefangenschaft gehaltenen Tieren von *Pitymys duodecimcostatus* wurde das Verhalten beim Graben untersucht. Die dabei aufgezeigten Verhaltensmuster unterscheiden sich von denen in früher veröffentlichten Arbeiten. 9 verschiedene Verhaltensmuster wurden untersucht, von denen 5 mit der

Grabaktivität in direktem Zusammenhang stehen. Die übrigen sind unabhängig davon. Die Abfolge der Grabvorgänge wurde anhand dieser 5 Verhaltensmuster untersucht. Das beim Graben gezeigte Verhalten zeigte einige Unterschiede zwischen den Geschlechtern auf und scheint von der Festigkeit der ausgegrabenen Erde abzuhängen. Die Ergebnisse zeigen, daß *Pitymys duodecimcostatus* bei hartem Substrat die Schneidezähne benutzt und damit ein ähnliches Verhalten wie *Arvicola terrestris* aufweist.

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A reconstruction of the Lava mouse (*Malpaisomys insularis*), an extinct rodent of the Canary Islands

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Abstract

Described the skeleton and evaluated the form, size and ecological niche of *Malpaisomys insularis*, an extinct rodent of the Canary Islands. The lava mouse was a generalized murid rodent with a head and body length of about 110 mm and a slightly shorter tail. Fore and hind limbs exhibit some adaptations for climbing, a favourable condition in its main habitat, the malpaís. There is a notable convergence in skeletal proportions between the lava mouse, the rock mouse (*Apodemus mystacinus*), the Galapagos rice rat (*Nesoryzomys narboroughi*), and other petricolic rodents which share(d) a similar creviscular habitat. The reasons for the extinction of *Malpaisomys* remain obscure. Data from Fuerteventura show that house mice arrived shortly before 2000 B. P.; from that time on to present a population decline of *Malpaisomys* and a contemporaneous increase of *Mus* is documented. Possibly the newly arrived house mice carried a desease which may have contributed to the extinction of the native mouse. This is indirectly suggested by a recently described rodent flea, for which the lava mouse may have been the original host rather than the introduced house mouse.

Introduction

The lava mouse (*Malpaisomys insularis*) is an endemic Canarian rodent recently discovered in subfossil deposits and archaeological sites of Fuerteventura, Lanzarote and Graciosa (Hutterer et al. 1988). Together with the shrew *Crocidura canariensis*, this rodent formed the native Holocene terrestrial small mammal fauna of the eastern Canary Islands. Two thousand years ago *Malpaisomys insularis* was extremely common, at least in Fuerteventura, where innumerable bones were recovered in the Cueva Villaverde (Hutterer et al. 1988). It is not known why such a successful rodent became extinct within a few centuries, even more because obvious causes such as competition with the black rat do not hold; our data document the absence of black rats during the extinction process. In order to understand what happened in the past, we have analysed the isolated bones of *Malpaisomys* and, by comparison with a variety of extant rodent species, tried to gain some information on its lifestyle from them. The aim of this paper therefore is first to present a skeletal reconstruction of the lava mouse, secondly to establish its morphological adaptations and to evaluate its ecological niche, and finally to consider the problem of its extinction.

Material and methods

The main part of the skeletal material of *Malpaisomys* used during this study was collected in July 1988 by three of us (R. H., N. L.-M., J. M.) during an excavation of the Cueva Villaverde (Fuerteventura), a project directed by the archaeologists F. Hernández and M. D. Sánchez. We used dry and wet screening with meshes of three different sizes. In addition we used the material already mentioned in the description of the genus (Hutterer et al. 1988). After cleaning and sorting representative samples of the larger skeletal bones were measured, as shown in Figure 1. Camera lucida drawings were made from well preserved bones and used for the reconstruction of the skeleton (Fig. 1). As all our material

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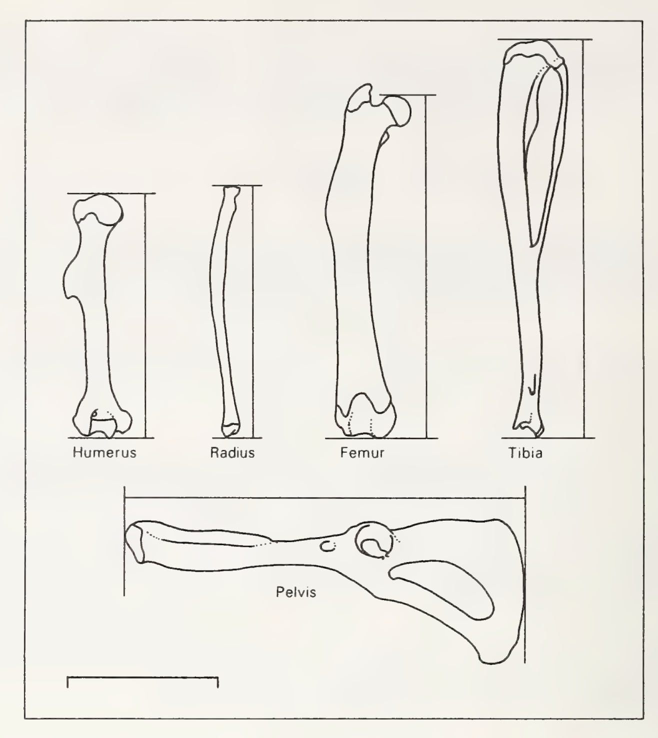


Fig. 1. Definitions of the main measurements taken for this study. Drawn after material of *Malpaisomys insularis* from Fuerteventura. (Scale = 10 mm)

consists of isolated bones, the number of vertebrae could not be accurately determined; however, there is no reason to believe that *Malpaisomys* deviates from other Murinae which normally have 7 cervical, 13–14 thoracic, 6–7 lumbar and 2–4 sacral vertebrae (Niethammer and Krapp 1978; Carleton and Musser 1984). For the purpose of comparison skeletons of 14 extant rodent species were prepared and measured (see Table); some data were also taken from Rausch (1976) and from Boye (1988). Complete skeletons of fossil Muridae are very rare; we studied an almost complete skeleton of *Paraethomys* cf. *miocaenicus* from Upper Miocene diatomites of Hellin, Spain (figured in Calvo et al. 1978) in the collections of the Department of Palaeontology, University of Madrid, and we used the information on the Pliocene *Apodemus atavus* given by Rietschel and Storch (1974). For a description and nomenclature of the bones of the postcranial skeleton of a rodent we refer to Schich (1971).

Results and discussion

Size and form of *Malpaisomys*

The lava mouse was large, comparable in body size with the rock mouse *Apodemus mystacinus*. Our reconstruction of the skeleton (Fig. 2) shows an animal of about 110 mm head and body length. The vertebral column is little modified and the dorsal and lateral processes are small. The processus spinosus of the epistropheus is rather small. A hypertrophied neural spine is not present on the second thoracic vertebra. There are three sacral vertebrae, the first two of which are usually fused. Their transversal appendices leave space for two pairs of round foramina sacralia.

Scapula, humerus, radius and ulna are similar to any species of *Apodemus*, except for their dimensions which will be discussed below. The same applies to the pelvis, femur and tibia. The tibia appears rather long and the crista tibialis is strongly developed, apparently

providing space for a large musculus flexor hallucis and musculus flexor digitorum, both of which are responsable for the flexibility of the toes. Also the musculus popliteus inserts at the crista tibialis. This muscle counteracts a rotation in the knee-joint, which is advantageous for a climbing animal. 54.3 % of the fibula length are not fused with the tibia.

The hindfoot length is difficult to estimate from isolated bones, but judged from the length of the calcaneus and the metatarsale (Fig. 2), it may have been about 26 mm.

Estimation of the tail length presented a problem. We finally found a simple solution for this problem, as demonstrated in Figure 3: plotting the known tail length of 14 species of murids (see Table) against the width of the second sacral vertebra (where tail-supporting muscles insert) gives a clear linear relation, which afterwards could be used to estimate the unknown tail length of *Malpaisomys* and other extinct rodents. For the lava mouse (mean width of the second sacral vertebra = 6.1 mm) we estimated a tail length of ca. 105 mm.

The body weight of the lava mouse was about 40 g. This calculation is based on the relation between head and body length and body weight of 34 species of European rodents (raw data were taken from NIETHAMMER and KRAPP 1978, 1982). The relation is highly significant ($r^2 = 0.95$, $n = 34$); a calculation for a head and body length of 110 mm resulted in a body weight of 37.9 g, which is very near to the weight of *Apodemus mystacinus* (40.9 g).

Biological data

In a previous paper (HUTTERER et al. 1988) we have mentioned that length measurements of 100 mandibles of lava mice show a bimodal distribution, if age classes are treated separately, which indicates a pronounced sexual dimorphism. There is more evidence for this assumption in the skeleton: the pelvis shows the same differences in shape (Fig. 4) that BECKER (1954) described for males and females of 8 European mice and voles. The os pubis is prolonged in females, while in males it is shorter and the ischium is broader.

Of the mandibles (from a level older than 1730 B.P.) measured, 27.8 % were classified as belonging to age class 1 (juvenile), 55.5 % to age class 2 (subadult to adult) and 16.7 % to age class 3 (old adult). We found similar values for *Mus musculus* from recent owl pellets from Lanzarote: of 100 mandibles 33 % belong to age class 1, 58 % to age class 2 and 9 % to age class 3. As the present-day house mice in the Canary Islands live in evidently viable

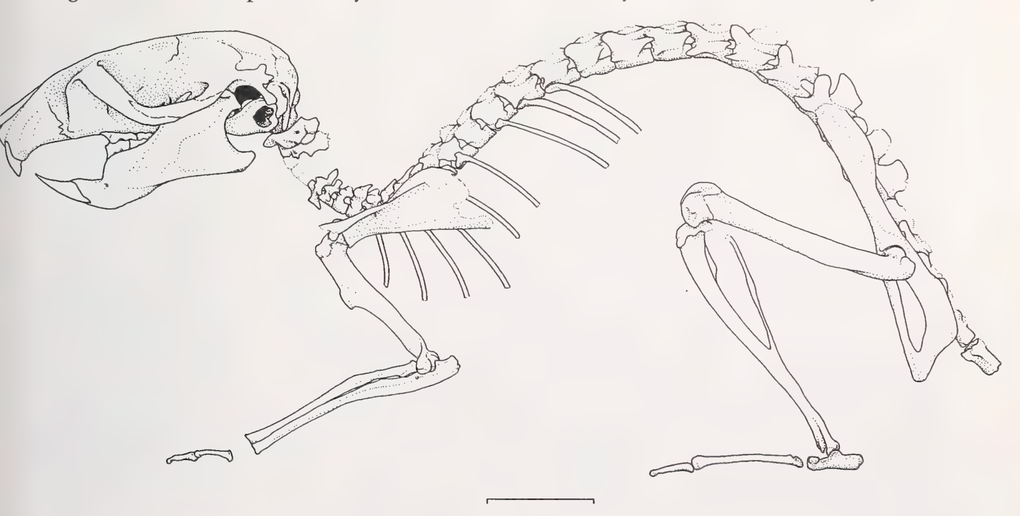


Fig. 2. Skeleton of the lava mouse *Malpaisomys insularis*, reconstructed from isolated bones from Cueva Villaverde, Fuerteventura. All elements shown have been found; most of the tail has been ommitted. (Scale = 10 mm. Drawn by P. BOYE)

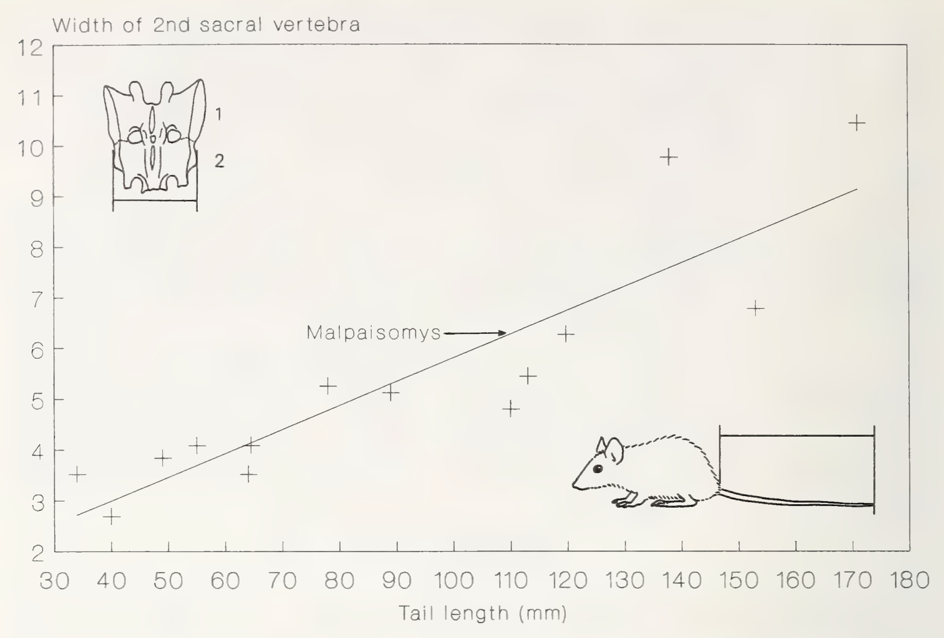


Fig. 3. The relation between tail length and width of the second sacral vertebra in 14 species of extant rodents; the width of the second sacral vertebra in *Malpaisomys* points to a tail length of about 105 mm

populations, we may draw the same conclusion for the ancient population of the lava mouse. At least we found no evidence for a limited viability, also no teratological bones and no tooth malformations. However, we have not yet sorted and examined all the material from all levels of the cave; therefore these comments must be taken as preliminary.

Foraging category and ecological niche

The skeleton of the lava mouse seems to represent a rather general type of murid with no special adaptations. However, if we compare its limb proportions with a set of living rodents for which the ecology is known, the picture becomes different. Figure 5 shows the relation between head and body length and the physiological fore limb length (humerus + radius) and hind limb length (femur + tibia) for a population of the terrestrial *Mus musculus*, and for two species of petricolic rodents, the Spiny mouse *Acomys dimidiatus* and the rock mouse *Apodemus mystacinus*. The diagram shows that both fore and hind limbs are relatively longer in the petricolic mice, and longest in the rock mouse, a species which lives in karstic rock fissures of the Mediterranean and Asia Minor. The petricolic snow vole *Microtus nivalis* (not shown in figure) also groups nicely near *Acomys* and *Apodemus mystacinus*; this vole is a good climber in rock fissures (Boye 1989).

The mean values for *Malpaisomys* fall into the range of *Apodemus mystacinus*. The same applies to *Nesoryzomys narboroughi* (not shown in the graph), a lava-dwelling rat endemic to the Galapagos Islands. We have compared the limb bones of *Malpaisomys* with those of *Nesoryzomys* and *Apodemus mystacinus* and found them to be very similar. The bones of *Nesoryzomys* (a member of the Sigmodontinae) are somewhat more heavily built, but those of *A. mystacinus* and *Malpaisomys* are almost indistinguishable.

Subterranean or fossorial rodents (Table; not shown in the graph) group far below the line for the terrestrial *Mus musculus*.

Selected measurements of skeletal elements

Species	Pelvis	Femur	Tibia	Humerus	Radius	HB	n
				unclassified extinct species			
Malpaisomys insularis	26.2	22.4	25.5	16.4	17	(110)	4–20
Paraethomys miocaenicus	17.2	16.7	20.6	12.0	13.1	(105)	1
				scansorial			
Micromys minutus	11.8	10.0	13.3	8.2	8.9	62.9	2
Grammomys caniceps	19.1	17.3	20.8	13.1	12.5	97	2
Apodemus sylvaticus	16.9	16.1	20.6	12.4	12.3	90.1	8
Apodemus flavicollis	22.1	20.3	25.0	15.5	15.3	107.5	2
				petricolic			
Apodemus mystacinus	23.6	22.5	27.8	16.6	16.9	111.7[a]	15
Acomys dimidiatus	21.7	18.8	22.3	14.3	13.4	105	1
	–	19.4	22.0	15.1	14.1	104.6	20[b]
Microtus nivalis	21.2	17.9	21.9	15.4	14.7	113.9	11
				terrestrial			
Mus musculus	15.5	12.8	15.8	10.0	10.4	73.5	1
	–	15.5	18.1	12.3	11.4	93.3	20[b]
Microtus agrestis	16.8	13.7	17.8	12.4	12.0	98.7	14
Clethrionomys glareolus	16.5	13.9	17.8	12.4	11.5	91.3	7
Apodemus agrarius	13.5	14.7	17.8	11.6	11.2	93	2
Arvicanthis niloticus	38.5	30.9	32.4	22.9	20.7	174.3	4
				fossorial			
Spalax leucodon	27.5	21.5	22.1	21.2	17.2	170	1
Arvicola terrestris	27.2	21.2	23.7	18.8	16.7	138	1

[a] Niethammer and Krapp (1978). – [b] Laboratory strains (Rausch 1976).

The Miocene rodent *Paraethomys* cf. *miocaenicus* (Fig. 5) goes along with *Mus*, as does the Pliocene *Apodemus atavus* (not shown in figure) for which species we took the measurements from Rietschel and Storch (1974). These two extinct species show a rather unspecialized condition, which we regard as primitive within the Muridae. This does not necessarily mean that all fossil rodents were primitive; Schmidt-Kittler and Storch (1985) described a skeleton of an Oligocene 'sand rat', *Pseudoltinomys* (Therdomyidae), and Koenigswald et al. (1988) showed that in the Eocene there lived already highly specialized arboreal rats such as *Ailuravus* (Paramyidae).

The limb proportions of *Malpaisomys* strongly suggest that the species was a good climber in rock fissures. This coincides perfectly with the sites where we found fossils of lava mice in the Canary Islands. Most were in somewhat weathered lava fields of Tertiary or Quaternary age, for which the Canarian people use the term 'malpaís'. Our main locality, the Cueva Villaverde, is a lava tube in the midst of such an ancient lava field. Only

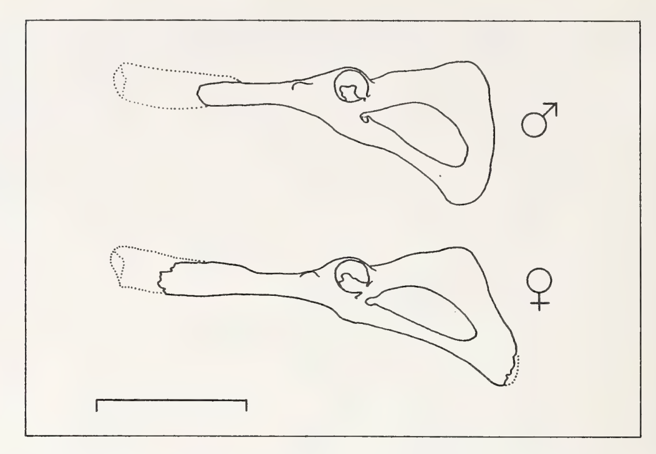


Fig. 4. Malpaisomys insularis, sexual dimorphism in the shape of the pelvis. Material from Malpais de Arena, Fuerteventura. (Scale = 10 mm)

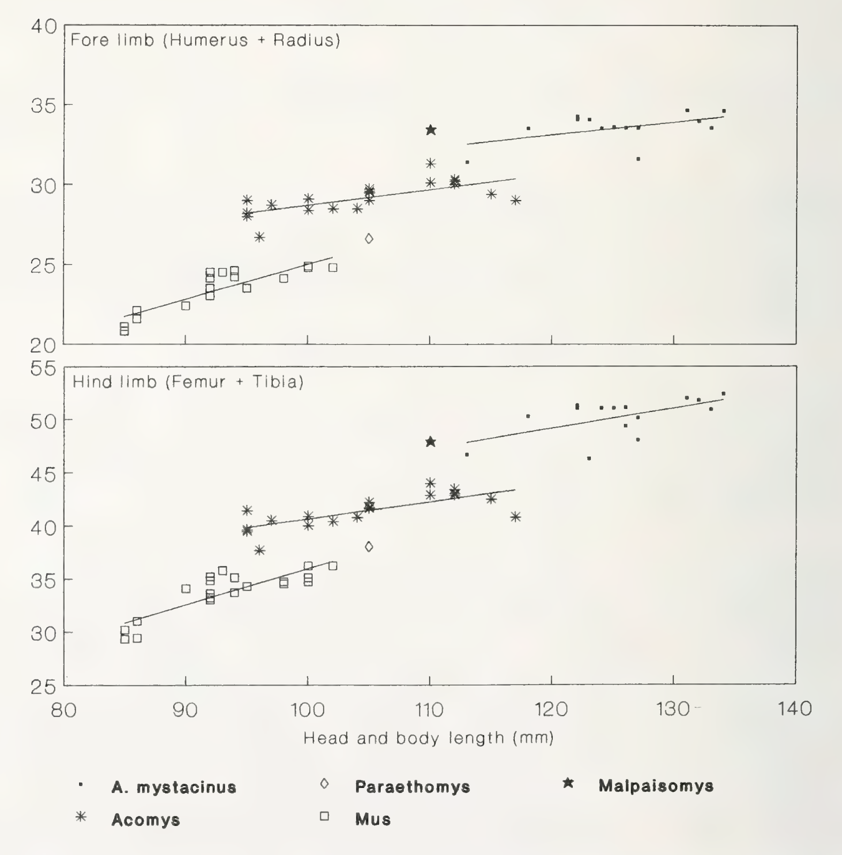


Fig. 5. Head and body length plotted against fore and hind limb length for populations of *Mus musculus, Acomys dimidiatus* (data from Rausch 1976) and *Apodemus mystacinus* (own data); the values for *Malpaisomys insularis* and the Miocene *Paraethomys* cf. *miocaenicus* are indicated

two localities in the Jandia peninsula (Fuerteventura) are different; there the fossils were found below a steep cliff, in the upper parts of which relict plants grow which are dependent upon high humidity. At the base of this mountain cliff there are large rock rubble piles which would provide a suitable fissure system for petricolic small mammals. However, traps set there for small mammals in July 1989 by one of us (R. H.) yielded no catches at all. In another locality in the Jandia peninsula we found fossils of lava mice in Pleistocene dunes (MICHAUX et al. 1991).

There is no indication that the former habitat of *Malpaisomys* was much different from the present-day malpais. We therefore hypothesize that the species had its ecological niche in the malpais zones of Fuerteventura, Lanzarote and adjacent islets, and that its morphological adaptations favoured living and climbing in the creviscular system of the lava fields. It only had to share this habitat with the endemic shrew *Crocidura canariensis* (HUTTERER et al. 1987), at least until the date when the house mouse arrived.

The extinction of *Malpaisomys*

From our most ancient fossil localities in Fuerteventura and Lanzarote we know that the native terrestrial small mammals of the eastern Canary Islands were *Malpaisomys insularis* and *Crocidura canariensis* (HUTTERER et al. 1988; MICHAUX et al. 1991). Our oldest samples from the Cueva Villaverde comes from a level underlying a horizon dated 1730 B.P. (HERNÁNDEZ and SÁNCHEZ 1986; CARRASCOSA and LÓPEZ-MARTÍNEZ 1988); in this sample *Malpaisomys* constitutes 58.9 % of the mammals, *Crocidura canariensis* 38.9 %, and *Mus musculus* 2.2 %. In the levels of younger age the proportion of *Mus* increases drastically (CARRASCOSA and LÓPEZ-MARTÍNEZ 1988), although no quantitative counts of all mammals are available for the moment. However, the data are sufficient to show that House mice occurred in Fuerteventura in very low numbers at 1730 B.P., and that they presumably arrived in the island a few centuries before, say 2000 B.P.

This was approximately the time when man arrived in the Canaries from neighbouring Africa. ONRUBIA PINTADO (1987) has shown that there are no absolute datations of archaeological sites in the Canaries older than 2490 B.P. (Tenerife: Barranco Hondo) and 1890 B.P. (Gran Canaria: Los Caserones). A fossil dune deposit with remains of endemic Giant rats, but without archaeological context (erroneously cited as such by ONRUBIA PINTADO 1987) at La Aldea, Gran Canaria, was dated as 2080 ± 60 B.P. (Cologne Radiocarbon Laboratory reference number KN-3542; this date was mentioned without source by LÓPEZ-MARTÍNEZ and LÓPEZ-JURADO 1987). This dune deposit also yielded one skull and one mandible of *Mus musculus*, which further supports our assumption of the arrival of house mice in the Canary Islands around 2000 B.P. The contemporary arrival of man strongly suggests a casual import of mice with ships from Africa.

Figure 6 shows that in a sample from historical times (ca. 800 B.P.; goat and rabbit were already present) the percentage of *Malpaisomys* is only 10.9 % while that of *Mus* is now 60.7 %. In two modern barn owl pellet collections shown in the same figure, the percentage of *Mus* is 95 and 87.4 %, while *Malpaisomys* is absent.

From our yet limited data we conclude that the populations of the lava mouse declined since the arrival of house mice about 2000 years ago, and were progressively replaced by them. We also show that black or brown rats (*Rattus rattus, R. norvegicus*) were not present during the extinction process, and – surprisingly – are even absent in recent owl pellets from arid regions of Fuerteventura. Today the black rat exists in Fuerteventura in cultures and villages, but seems to avoid the open plain and the lava fields. Apparently it was introduced quite recently.

Our present data suggest that for almost two millennia *Malpaisomys* and *Mus* were the only rodents in Fuerteventura. It is therefore possible that interactions between these two species have caused the extinction of the lava mouse. Other factors like climatic changes or

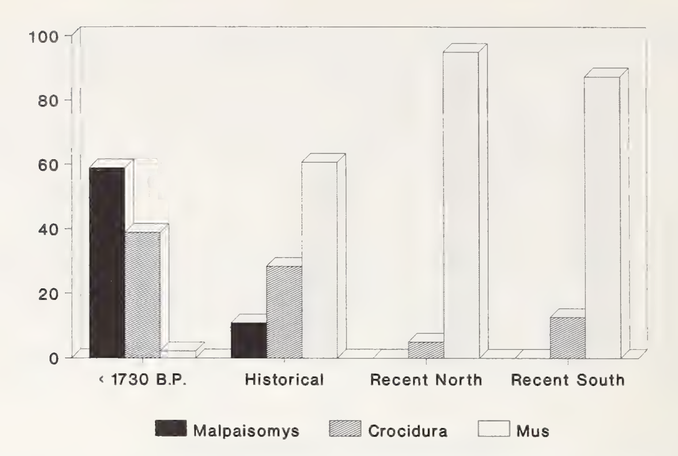


Fig. 6. The percentages of micromammals in fossil and recent barn owl pellets from Fuerteventura. From left to right: Cueva Villaverde, level older than 1730 B.P. (n = 764); Malpais de Arena, Historical period, ca. 800 B.P. (n = 183); Villaverde, recent barn owl pellets (n = 240); Barranco de la Torre, recent barn owl pellets (n = 111)

volcanic activities may have added to this process, but these variables are unsufficiently documented. However, Carrascosa and López-Martínez (1988) have shown that the house mouse suffered some loss in size from about 2000 B.P. to present, which indicates environmental changes. On the other hand the shrew *Crocidura canariensis* survived from the Pleistocene (Michaux et al. 1991) into our times and still occurs in high numbers in the malpais.

What remains is the fact that the numbers of lava mice declined and those of house mice increased. Direct competition between the two rodents seems unlikely, as they represent two distinct size classes. We consider the possibility of an indirect impact of house mice on lava mice, for example through a fatal disease carried by the house mice and consequently transmitted to the formerly isolated lava mice.

Indirect evidence for a contact between both may be taken from a paper on fleas of extant Canarian rodents by Beaucournu et al. (1989). They described a new flea, *Xenopsylla guancha*, which they collected from house mice in Lanzarote; it was not found in other islands of the archipelago and not previously in the (well-studied) north-western parts of Africa. According to the authors, the new flea is related to North African species for which gerbils are the main hosts; therefore they discuss the possible existence of a vanished gerbil in the Canaries.

According to our data house mice arrived in the Canary Islands only 2000 years ago. There is no evidence for gerbils but for *Malpaisomys* in Lanzarote and Fuerteventura. Probably the lava mouse was the original host of the flea *Xenopsylla guancha*, which later changed to the house mouse and survived there after its native host had vanished.

Acknowledgements

Our field campain in 1988 was made possible by the invitation of F. Hernández and M. D. Sánchez to participate in their archaeological excavation of the Cueva Villaverde. We also thank the Ayuntamiento de La Oliva for permissions and support. J. Freundlich (C14-Labor, Universität Köln) kindly provided the radiocarbon datations. We are grateful to J. Adrian, technical assistent of the Museum Alexander Koenig, for his careful work of sorting, cleaning and preparing the fossils and skeletons, to S. von Groll for supplying us with a series of *Apodemus mystacinus*, and to G. Peters for linguistic improvements. This paper was first presented at the 5th Symposium "Fauna and Flora of the Cap Verde Islands" at Leiden, The Netherlands, October 1989.

Zusammenfassung

Eine Rekonstruktion der Lavamaus (Malpaisomys insularis), einem ausgestorbenen Nager der Kanarischen Inseln

Anhand von subfossilen Knochenresten wurde das Skelett der Lavamaus *Malpaisomys insularis* rekonstruiert und ihr Körperbau, ihre Körpergröße und ökologische Nische abgeschätzt. Die Lavamaus entsprach einem generalisierten Muriden; die Kopf-Rumpflänge betrug ca. 110 mm, der Schwanz war etwas kürzer. Die Vorder- und Hinterextremitäten waren verlängert, eine Anpassung an die kletternde Lebensweise in den Lavawüsten der Kanarischen Inseln. Die Skelettproportionen sind bemerkenswert ähnlich denen der Felsenmaus (*Apodemus mystacinus*), der Galapagosreisratte (*Nesoryzomys narboroughi*) und anderer felsbewohnender Nager, die ebenfalls in dreidimensionalen Habitaten leben. Die Gründe für das Aussterben der Lavamaus in historischer Zeit sind unklar. Daten aus Fuerteventura belegen, daß die Hausmaus (*Mus musculus*) auf dieser Insel um 2000 B.P. eintraf; von da an läßt sich in subfossilen Eulengewöllen eine Abnahme von *Malpaisomys* und eine Zunahme von *Mus* belegen. Möglicherweise infizierten Hausmäuse die Lavamäuse mit unbekannten Krankheiten; indirekt weist darauf ein nur von Lanzarote bekannter Floh hin, der von Hausmäusen abgesammelt wurde. Da Hausmäuse erst in historischer Zeit dort eingewandert sind, kommt als natürlicher Wirt nur die Lavamaus in Frage.

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A new species of Spiny rat genus *Proechimys*, subgenus *Trinomys* (Rodentia: Echimyidae)

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Abstract

Described a new species of spiny rat genus *Proechimys*, subgenus *Trinomys* based on seven specimens collected in Conceição do Mato Dentro, state of Minas Gerais, southeastern Brazil. The diagnostic characters of the new species are an elongate and posteriorly wide incisive foramen and a baculum with weakly developed apical wings. This new species differs from previously described species of the subgenus by a set of characters including the color of the pelage and skull, teeth, and bacular morphology.

Introduction

The genus *Proechimys* comprises the subgenera *Proechimys* Allen, 1899 and *Trinomys* Thomas, 1921 which are distinguished by a series of cranial, dental, and body traits. In the subgenus *Trinomys* the main fold of the molariform teeth extends entirely across the worn crown and the size of teeth decreases progressively from the premolar to the third molar. The ridges of the skull are moderately developed, and the infraorbital foramen lacks a groove for transmission of the nerve (Moojen 1948). The two subgenera have disjunct distributions, with the subgenus *Proechimys* ranging from Nicaragua to northern Paraguay, whereas the subgenus *Trinomys* occurs in the Atlantic forest of eastern Brazil (Fig. 1).

Four species are currently recognized for the subgenus *Trinomys*, namely *Proechimys dimidiatus* (Günther, 1877), *Proechimys iheringi* Thomas, 1911, *Proechimys setosus* (Desmarest, 1817) and *Proechimys albispinus* (Geoffroy, 1838). A fifth species, *Proechimys myosurus* (Lichtenstein, 1830), was thought by Moojen (1948) to be related to *P. albispinus* or even a synonym of this form. The monograph by Moojen (1948) has remained a unique source for the study of systematics in the subgenus *Trinomys*. We have started a detailed analysis of the variation and systematics of this subgenus (Pessôa 1989; Pessôa and Reis 1990; Reis et al. 1990; Pessôa and Reis 1991a, b, c, d; Reis et al. 1991) and have come upon a species distinguishable from all the forms so far recognized for *Trinomys*. In the present study, we describe this new form of *Proechimys* from the state of Minas Gerais, Brazil.

Material and methods

The specimens of *Proechimys dimidiatus*, *P. iheringi*, *P. setosus*, and *P. albispinus* used for comparisons with the new species were identified with the aid of Moojen's (1948) diagnoses for cranial and pelage characteristics. Hair terminology follows Moojen (1948) and hair measurements were taken with an eyepiece micrometer. Capitalized color definitions follow Ridgway (1912). Cranial measurements defined by Moojen (1948) were taken with digital calipers graduated to 0.01 mm, and external measurements (length of head and body, length of tail, length of hind foot, and length of ear) were

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obtained from skin tags. Descriptions of bacular morphology were taken from Pessôa and Reis (1991d).

Specimens examined are housed in the Museu Nacional (MN), Museu de História Natural da Universidade Federal de Minas Gerais (MHN), and Museu de Zoologia da Universidade de São Paulo (MZUSP), and are listed as follows: *Proechimys dimidiatus* (Rio de Janeiro: Tijuca [MN 10344, 10355, 10359, 10362, 10366, 10367, 12814]); *Proechimys iheringi iheringi* (São Paulo: Ilha de São Sebastião [MZUSP 218, 221, 222, 2095, 2145, 2146, 2525, 3201, 10072]); *Proechimys iheringi bonafidei* (Rio de Janeiro: Teresópolis [MN 6179, 6181–6183, 6187, 6780, 6782, 6784, 6786, 6787]); *Proechimys iheringi gratiosus* (Espírito Santo: Floresta da Caixa Dagua [MN 4018, 5430, 5656, 5674, 5757, 5759, 5767, 5772]); *Proechimys iheringi paratus* (Espírito Santo: Capela de São Braz [MN 4012, 4023, 5455, 5458]); *Proechimys iheringi panema* (Espírito Santo: Campinho [MN 8284–8288]); *Proechimys iheringi denigratus* (Bahia: Itabuna [MN 10474, 10476, 10477, 10515, 10517, 10519, 10521, 10523–10525, 10528]); *Proechimys albispinus* (Bahia: Jequié [MN 13966, 13967, 13969, 14009, 14012, 14013, 14016]); *Proechimys setosus* (Minas Gerais: Santa Bárbara [MHN 131, 149, 870]).

Results

Proechimys moojeni, new species

Holotype: 13380, MN; skull and skin of an adult female specimen; collected by Cory T. Carvalho, field number 138, on 25 August 1954.

Type locality: Mata do Dr. Daniel, Conceição do Mato Dentro, Minas Gerais, Brazil; 19° 01'S, 43° 25'W (Fig. 1).

Other specimens: Six skins and skulls, three from Mata do Dr. Daniel and three from Boca da Mata in Conceição do Mato Dentro.

Distribution: Known only from the type locality.

Diagnosis: A *Proechimys* distinguished from all previously described species of the subgenus *Trinomys* by the presence of an elongate and posteriorly wide incisive foramen, two counterfolds in upper and lower molariform teeth, baculum with weakly developed apical wings.

Description

Pelage. – Aristiforms on middorsal region: grayish basally, gradually blackening toward tip; total length (mean = 20.35, range = 19.04–21.98); maximum width (mean = 0.63, range = 0.45–0.73). Aristiforms on outer thighs: Two color types of aristiforms, both whitish basally, becoming gray in the median part, one Ochraceous Buff through the tip and the other gradually blackening toward the tip; total length (mean = 15.85, range = 14.02–18.84); maximum width (mean = 0.46; range = 0.35–0.66). Setiforms on middorsal region: whitish basally, gradually blackening toward tip but interrupted by an Ochraceous Orange subapical zone 2.35 to 5.85 long (mean = 3.89); total length (mean = 17.09, range = 15.58–18.78); maximum width (mean = 0.14, range = 0.13–0.15). Setiforms on outer thighs: Gray basally, gradually blackening toward tip interrupted by an Ochraceous Orange subapical zone 2.12 to 3.60 long (mean = 2.78); total length (mean = 13.27, range = 11.85–15.27); maximum width (mean = 0.12, range = 0.10–0.15). General color on upper parts and sides orange brown due to a combination of blackish from the tips of aristiforms and Ochraceous Orange ground color from the subapical zone of setiforms. Differentiated light-colored aristiforms on outer sides of thighs and rump. Tail bicolored, white below and brown above in the anterior two-thirds, tail tip white (Fig. 2).

Skull. – Elongate and slightly convex; bullae small and smooth; rostrum short but not stout; transverse ridge of jugal bones not well developed; postorbital process of zygoma well developed and formed by jugal and squamosal bones; incisive foramen elongate and posteriorly wide; vomerine sheath incomplete and formed almost exclusively by premaxillae; maxillary part of the vomerine sheath short; posterior palatine foramina at anterior plane of first molars; mesopterygoid fossa extending forward as far as the anterior plane of second molars (Fig. 3). Skull and body measurements are given in Table 1.



Fig. 1. Map showing the distribution of the two subgenera of the genus *Proechimys* (after MOOJEN, 1948). The black star denotes the type locality of the new species of *Proechimys*

Teeth. – Incisives orthodont, upper and lower molariform teeth with two counterfolds (Fig. 4).

Baculum. – Elongate and narrow with a straight shaft. Shaft with a slight dorsoventral curvature and a tappered lateral indentation near mid-shaft. Proximal end straight and paddle-shaped. The distal end has weakly developed apical wings (Fig. 5).

Comparisons: *Proechimys moojeni* shares with *P. iheringi, P. albispinus*, and *P. setosus* the aristiform hairs wide and stiff as opposed to *P. dimidiatus,* whose aristiforms are narrow and soft. The tail is shorter in *P. moojeni, P. dimidiatus,* and *P. albispinus,* and longer in *P. iheringi* and *P. setosus,* where it is associated with a penicillated tip. *Proechimys moojeni, P. dimidiatus,* and *P. iheringi* have longer and slightly convex skulls, whereas in *P. setosus* and *P. albispinus* the skull is shorter and conspicuously convex. The incisive foramen is posteriorly constricted in *P. iheringi, P. setosus,* and *P. albispinus* and widest posteriorly in *P. dimidiatus* and *P. moojeni* (Fig. 6). The latter species differ by the length



Fig. 2. Study skin of the holotype of *Proechimys moojeni* (MN 13380)

Measurements (in mm) of adults of *Proechimys moojeni*

Specimen numbers	13366	13368	13372	13376	13379	13382	13380
Sex	F	M	M	M	F	M	F
Length of head and body	180	165	148	170	151	178	170
Length of tail	160	160	144	163	–	172	162
Length of hind foot	44	44	40	43	42	44	43
Length of ear	25	22	22	25	21.5	24	23
Greatest length of skull	51.2	50.7	45.6	51.8	51.2	50.6	50.4
Condylo-incisive length	36.6	34.8	31.7	36.6	36.1	35.6	35.4
Zygomatic breadth	26.5	25.2	24.5	25.9	25.4	24.4	25.0
Length of nasals	18.7	16.5	16.3	18.9	18.1	17.3	17.3
Interorbital constriction	12.0	12.2	10.7	12.3	12.3	12.0	11.8
Palatilar length	17.3	16.1	14.4	15.6	16.8	16.2	15.4
Length of upper toothrow	9.0	8.6	7.8	8.2	8.3	8.4	8.6
Length of incisive foramen	4.3	5.0	3.8	4.7	4.5	4.3	4.7
Width of incisive foramen	2.3	2.2	1.8	2.5	2.4	2.4	2.2

of the foramen, which is short in *P. dimidiatus* and longer in *P. moojeni.* In *Proechimys dimidiatus* the vomerine sheath is complete, whereas it is incomplete in *P. moojeni. Proechimys moojeni* always has two counterfolds in all molariform teeth in the specimens examined, whereas *P. albispinus* always shows one. The number of molariform counterfolds varies in the remaining species. In *P. dimidiatus* and *P. iheringi* this number varies from two to three, whereas in *P. setosus* it varies from one to two. The baculum in *P. moojeni* differs from *P. dimidiatus, P. iheringi* and *P. setosus* by the presence of apical wings. From *P. albispinus* it is distinguished by its smaller size and less developed apical wings (Pessôa and Reis 1991d).

Etymology: The name *moojeni* is given to honor Dr. João Moojen, whose outstanding and pioneer work laid the foundations for the study of the systematics and evolution of the genus *Proechimys*.

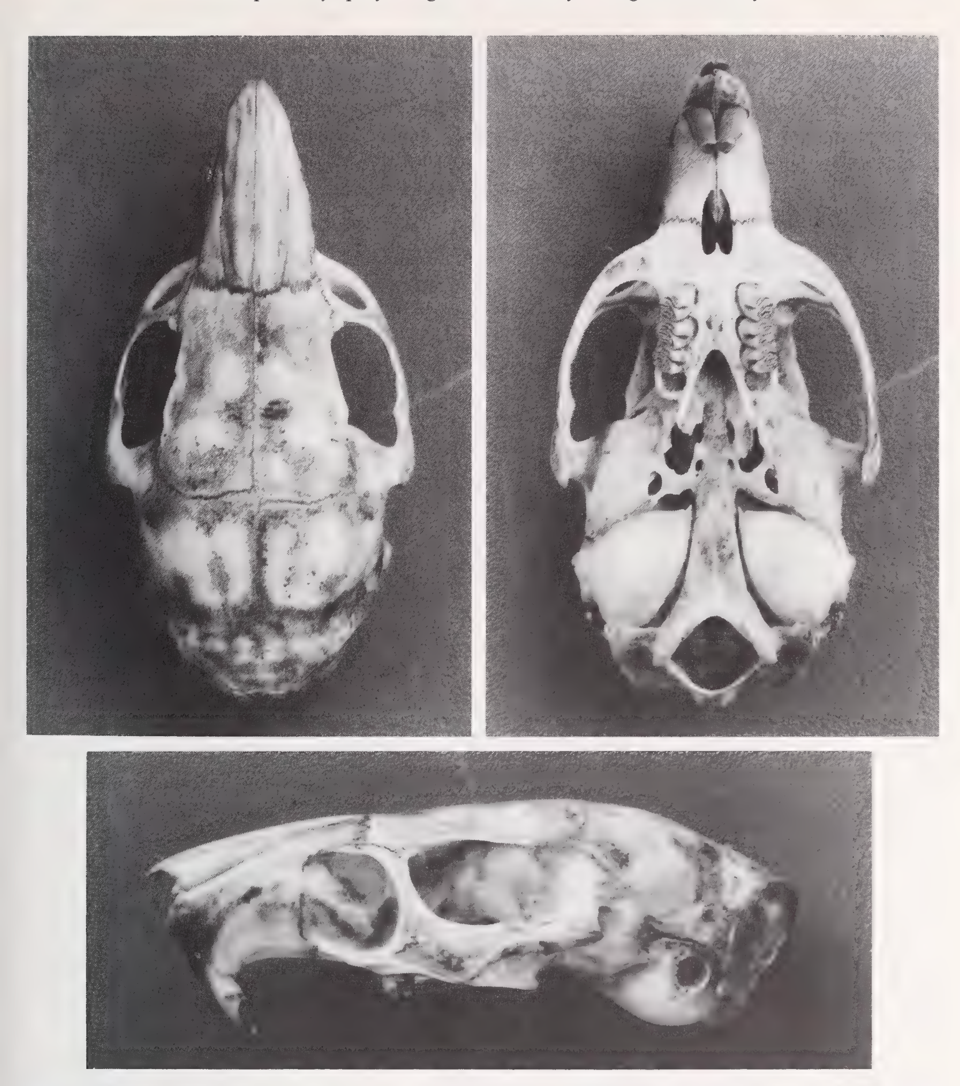


Fig. 3. Dorsal, ventral, and lateral views of the skull of the holotype of *Proechimys moojeni* (MN 13380)

Discussion

In his detailed systematic analysis of the genus *Proechimys,* Moojen (1948) defined the morphological limits of variation at the subgeneric, specific, and infraspecific levels. Moojen (1948) employed the thickness and color of aristiform hairs, the size and shape of the skull, the shape and structure of the incisive foramen, and the number of molariform counterfolds to define the limits of variation between species in the subgenus *Trinomys.* Moojen (1948) combined these traits to characterize the species of *Trinomys* and apparently no single character could uniquely diagnose the species in the subgenus *Trinomys.* Nevertheless, close inspection of the shape and structure of the incisive foramen allows the unambiguous recognition of each species. The premaxilla and the maxilla form a bridge



Fig. 4. Upper right molariform teeth of a paratype of *Proechimys moojeni* (MN 13379)

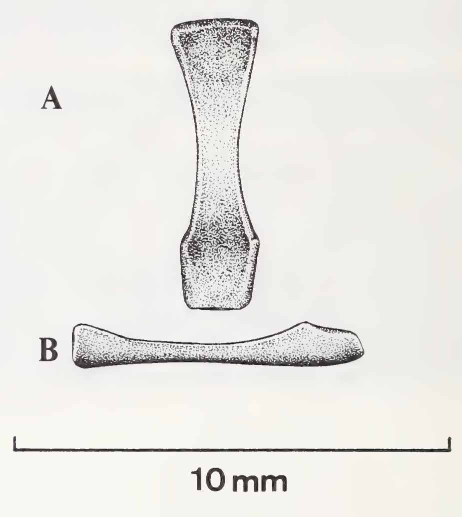


Fig. 5. Ventral (A) and lateral (B) views of the baculum of *Proechimys moojeni.* The distal part is put to the top (ventral view) and to the left (lateral view)

that crosses the incisive foramen longitudinally. The premaxillary part is always well developed, whereas the degree of development of the maxillary part shows considerable variation (Moojen 1948). A complete vomerine sheath occurs when the premaxillary and maxillary parts meet. In *P. dimidiatus* the vomerine sheath is complete and the maxillary part is wide and well developed. In *P. iheringi* the vomerine sheath can be either complete or incomplete with a short maxillary part. The vomerine sheath is complete in *P. setosus* and *P. albispinus.* The maxillary part is short and slender in *P. setosus.* The premaxillary part of the vomerine sheath in *P. albispinus* is on a level lower than that of the maxillary

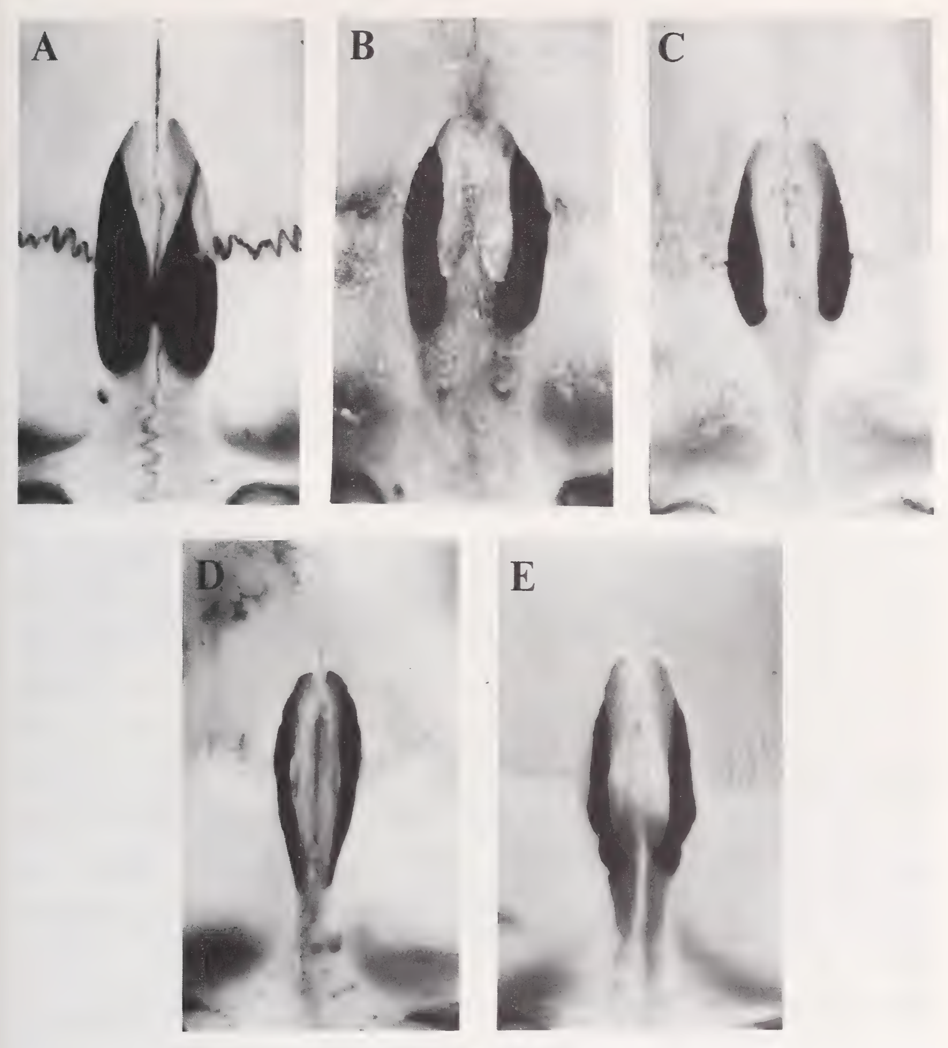


Fig. 6. Representative incisive foramina of species of the subgenus *Trinomys*, genus *Proechimys*. A: *P. moojeni*; B: *P. dimidiatus*; C: *P. iheringi*; D: *P. setosus*; E: *P. albispinus*

part, which is keeled. In *P. moojeni* the vomerine sheath is incomplete with a short maxillary part.

Recent studies have shown that bacular morphology can also be used to diagnose species of the subgenus *Trinomys* (Pessôa and Reis 1991d). Although several morphological characters have been combined to characterize the species of *Trinomys*, the shape and structure of the incisive foramen and the size and shape of the baculum are good characters to define species at the morphological level in this subgenus.

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Zusammenfassung

Eine neue Art von Stachelratten des Genus Proechimys, Subgenus Trinomys (Rodentia: Echimyidae)

Beschrieben wird eine neue Art der Stachelratten, *Proechimys* (*Trinomys*) *moojeni*. Die Typenserie umfaßt sieben Exemplare von Conceição do Mato Dentro aus dem Staat Minas Gerais in Südost-Brasilien.

Kennzeichnend sind vor allem lange und hinten breite Foramina incisiva sowie ein Baculum mit schwach entwickelten apikalen Flügeln. Außerdem unterscheidet sich die Art von den anderen, bisher bekannten *Proechimys*-Arten in der Fellfärbung, in der Zahnmorphologie und weiteren Merkmalen des Schädels und des Baculums.

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Habitat relations in sympatric populations of *Ctenomys australis* and *Ctenomys talarum* (Rodentia, Octodontidae) in a natural grassland

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Abstract

Studied the relationship between animal spatial distribution of two sympatric populations of "tuco-tucos" (*Ctenomys australis* and *Ctenomys talarum*) in Necochea (Buenos Aires Province, Argentina), and certain environmental variables. The two species occupy different types of soil and vegetation. *C. australis* inhabits areas with sparse vegetation, sandy and deep soils, while *C. talarum* inhabits areas with dense vegetation, compact and shallow soils. Seasonally, "tuco-tucos" are also associated with fine grain variables, as observed in autumn, where the total number of animals, and the number of *C. australis* individuals, were positively correlated with the abundance of grasses, perennials, plants with reserve organs and creeping habit plants.

Introduction

Biological factors such as interspecific interactions may play an important role in subterranean rodent distribution. There are very few documented cases of sympatry in subterranean rodents (Contreras and Reig 1965; Russell 1968; Reichman and Baker 1972; Williams and Baker 1976; Moulton et al. 1983; Pearson 1984). Vaughan (1967) suggested only one subterranean niche exists for herbivorous mammals. Subterranean mammal distribution, although sometimes parapatric, is seldom sympatric, and since parapatric distribution is determined by competition, it can be predicted that sympatry could be transitory (Moulton et al. 1979).

In the Southern Hemisphere, nearly all *Ctenomys* species ("tuco-tucos") present an allopatric distribution. In Argentina, only two cases of parapatry have been recorded (Pearson 1984; Reig et al. 1990); and only one case of sympatry was registered between *Ctenomys australis* and *Ctenomys talarum* in Buenos Aires Province, from Bahía Blanca to Monte Hermoso, where these two species occupy different soil and vegetation types (Contreras and Reig 1965). We discovered that this distribution extends up to Necochea and that *C. australis* does not live in allopatry in this area. The fact that this situation has been maintained over a long period (Contreras and Reig 1965), the different corporal sizes between *C. australis* and *C. talarum*, and the manifest spatial segregation between both species associated with different soil and vegetation types, all suggest that these populations coexist in sympatry, with non-overlapping niches. Corporal size differences between populations have been documented by Malizia et al. (in press), who determined that *C. australis* weighs three times *C. talarum*.

In the present study, the hypothesis was tested that *C. australis* and *C. talarum* occupy different habitats in the area of sympatry. In addition, it was determined whether different animal categories occupy different habitats according to sex, age and reproductive conditions.

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Material and methods

The present study was conducted in a dune natural grassland (Vervoorst 1967; Cabrera and Zardini 1978) in Necochea district (Buenos Aires Province, Argentina). The sampling period extended from November 1987 to September 1988. In each season, an area of approximately 2 ha was selected inside the overlap zone of both species. In the area studied in spring, distribution areas of *C. australis* and *C. talarum* were clearly delimited. In contrast, in summer, autumn and winter, the spatial distribution of both species in the chosen areas was more intermingled, showing greater heterogeneity than in spring. Vegetation samples and animals were taken toward the end of each season (November–December 1987, February–March, May–June and August–September 1988). In each area, a 10 by 10 m grid was traced. Vegetation samples were extracted systematically each 10 m. A soil block of 30 cm diameter and 30 cm depth was collected at each sample site. Then, samples were separated by hand in each species aerial and subterranean fractions. The material was dried at 80 °C, and the corresponding dry weights were obtained. A sample by species matrix (aerial plus subterranean biomass/species/sample) was constructed for each season. Twenty-four samples were obtained in spring, 24 in summer, 31 in autumn and 48 in winter.

Density and spatial distribution of both populations of "tuco-tucos" were estimated in a simultaneous study carried out in the same grids, by capture and extraction of all the animals present in the studied area (Table 1). Animal species, localization in the grid, age, sex, weight and reproductive condition were registered (Malizia et al. in press). Once during the duration of the study, soil hardness and soil depth overlying the calcareous layer were determined randomly. Twenty five measurements of soil hardness and depth were obtained with a penetrometer and a steel bar, respectively, in both species' zones.

Table 1. **Seasonal densities (individuals/ha) of *C. australis* and *C. talarum***

According to Malizia et al. (in press)

	Spring	Summer	Autumn	Winter
C. australis	7.4	4.5	4.0	4.6
C. talarum	10.7	12.7	17.0	4.6

To characterize the vegetation, different bionomic attributes relevant to vegetation spatial heterogeneity and plant-animal interactions were assigned to the plant species. The bionomic attributes considered were: perennity, presence of reserve organs, phenology, pilosity, growth form, presence in modified fields, taxonomic class. Besides ocular observation, the species descriptions of Cabrera and Zardini (1978), and Lombardo (1982, 1983, 1984) were consulted. With this information, a species by attributes matrix (floristic matrix) was created. This matrix was analysed complementing ordination (Principal Component Analysis, PCA, Harris, 1975) and classification (Cluster Analysis, CA, Orlóci, 1978) techniques so as to describe species variation and define species groups. The CA was performed with Nearest Neighbor distance estimator, simple linkage, and 1-Pearson correlation coefficient for sample distances. Table 2 shows a list of species present in the area grouped according to the analysis just described.

Each seasonal aerial plus subterranean biomass/species/sample matrix was multiplied by the floristic matrix, obtaining an attribute/sample matrix. The four seasonal matrices were appended so as to obtain an annual matrix of data. The importance of each attribute in the samples was also analysed complementing PCA and CA so as to describe the principal trends of vegetation heterogeneity. Sample groups were defined at a level of internal similarity $\geq$ to 80 %.

To determine which vegetation characteristics were associated with animal distribution, simple correlations were established between sample positions along the principal axes of ordination and the total number of captured animals, the number of *C. australis* individuals and the number of *C. talarum* individuals, at each sample site. Also, seasonal sample groups of vegetation, at each seasonal analysis, were related to animal categories which occupied such sites. SYSTAT statistical program was used to analyse data.

Results

Figure 1 corresponds to the annual analysis (samples taken in spring, summer, autumn and winter) and shows the spatial distribution of samples along the first two axes of the PCA on the samples/attributes matrix. All the vegetation variables included in the analysis had positive weights in axis 1, most of them having values over 0.7. Then, axis 1 separates samples with high from samples with low abundance of the plant attributes evaluated, and thus is interpreted as an index of vegetation coverage and density. According to this interpretation, the negative and positive extremes of the axis are denominated "sparse vegetation" and "dense vegetation", respectively. Samples with sparse vegetation have

Table 2. **Vegetation groups, according to ordination and classification techniques, from a dune natural grassland in Necochea district, Buenos Aires Province, Argentina, where *C. australis* and *C. talarum* show an overlap in their distributions**

Group	Attributes	Species
1	Forbs, Annuals, Cool season species, Pivotal roots, Without reserve organs, Present in modifield fields	*Geranium dissectum* *Lepidium bonariense* *Gamochaeta spicata* *Stellaria media* *Melilotus indicus* *Senecio madagascariensis* *Medicago minima* *Medicago lupulina*
2	Forbs, Perennials, Warm season species, Pivotal roots	*Convolvulus hermanniae* *Adesmia incana* *Mesembryanthemum* sp. *Oenothera mollisima* *Achyrocline satureioides* *Margyricarpus pinnatus* *Ambrosia tenuifolia* *Solidago chilensis*
3	Forbs and Grasses, Perennials, With reserve organs, Warm season species, Creeping habit	*Solanum commersonii* *Hydrocotyle bonariensis* *Calystelgia soldanella* *Panicum racemosum* *Paspalum vaginatum*
4	Grasses, Perennials, Glabrous	*Agrostis* sp. *Poa bonariensis* *Sporobolus indicus*
5	Grasses, Fibrous roots, Without reserve organs, Erect habit	*Bothriochloa laguroides* *Stipa neesiana* *Stipa trichotoma* *Bromus* sp. *Lolium multiflorum* *Poa annua* *Hordeum leporinum* *Catapodium rigidum* *Lophochloa phleoides*
6	Annuals, Grasses, Fibrous roots, Without reserve organs, Creeping habit	*Cenchrus pauciflorus*

sandy and deep soils (soil hardness 4.1 ± 0.9 kg/cm^2, and soil depth 80 ± 24 cm), while those with dense vegetation have compact and shallow soils (soil hardness 29.3 ± 8.1 kg/cm^2, and soil depth 57 ± 27 cm). Axis 2 opposes samples whose species attributes are typical of modified fields (annuals, cool season cycle, without reserve organs) to samples whose species attributes are typical of unmodified fields (perennials, creeping habit, with reserve organs). Three groups of samples were defined by CA: 1. Dense vegetation, with plant attributes characteristic of unmodified fields. 2. Dense vegetation, with plant attributes characteristic of modified fields. 3. Sparse vegetation, with plant attributes characteristic of modified and unmodified fields.

Total number of animals, as well as number of individuals of both *C. australis* and *C. talarum* showed a significant correlation ($P < 0.05$) with sample position along axis 1 of the PCA. Total number of animals and number of *C. talarum* individuals were positively correlated with the position of dense vegetation samples, and number of *C. australis*

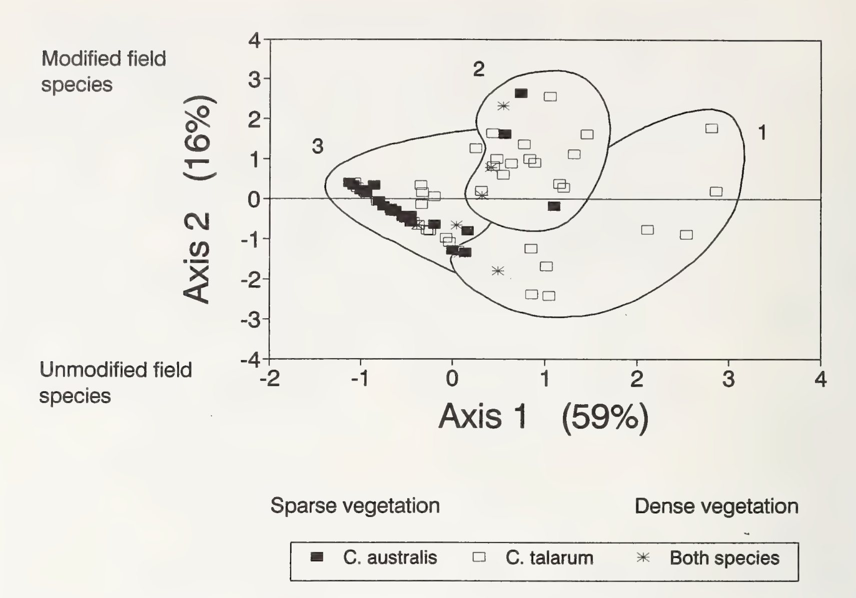


Fig. 1. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Annual analysis. Values in brackets show the percentage of the variance explained by each axis. Symbols indicate presence of *C. australis, C. talarum*, or both species, respectively. Samples without animals were excluded to simplify the diagram. Samples were grouped according to a CA on the referred matrix

individuals was positively correlated with the position of sparse vegetation samples. According to these results, two habitats were defined:

a. Typical *C. talarum* area: dense vegetation, compact and shallow soil;

b. Typical *C. australis* area: sparse vegetation, sandy and deep soil.

C. australis had a body weight three times that of *C. talarum* (males: 425.3 ± 19.8 g vs. 131.6 ± 17.2 g, and females: 297.7 ± 6.8 g vs. 98.7 ± 13.52 g) and a lower population density (5.15 ± 0.76 individuals/ha vs. 11.32 ± 2.56 individuals/ha), Malizia et al. (in press).

In the seasonal analysis, as in the annual one, the principal tendency in data variability (axis 1, PCA) shows a contrast between sparse and dense vegetation (Figs. 2, 3). Except in autumn, this contrast explains more than 60 % of the total variance. This shows that two environmental subsystems are clearly distinguishable. In autumn (axis 1 explains 47 % of total variance) the contrast is diluted (Fig. 2). The second tendency in autumn data variability (axis 2, PCA), as well as in the annual analysis, marks a contrast between species attributes typical of unmodified vs. modified fields: grasses, perennials, presence of reserve organs, and creeping habit, vs. forbs, annuals, pivotal roots, respectively. Although less marked, this second contrast also exists during the remainder of the seasons.

The CA of the autumn data shows four groups of vegetation (Fig. 2.): 1. Dense vegetation, with plant attributes characteristic of unmodified fields. 2. Dense vegetation, with plant attributes characteristic of modified fields. 3. Sparse vegetation, with plant attributes characteristic of modified and unmodified fields. 4. Sparse vegetation, mainly characteristic of unmodified fields.

The CA of the spring data shows two main sample groups (Fig. 3): 1. Dense vegetation. 2. Sparse vegetation. Both vegetation types have plant attributes characteristic of modified and unmodified fields. Only four samples are not included in the main groups as a

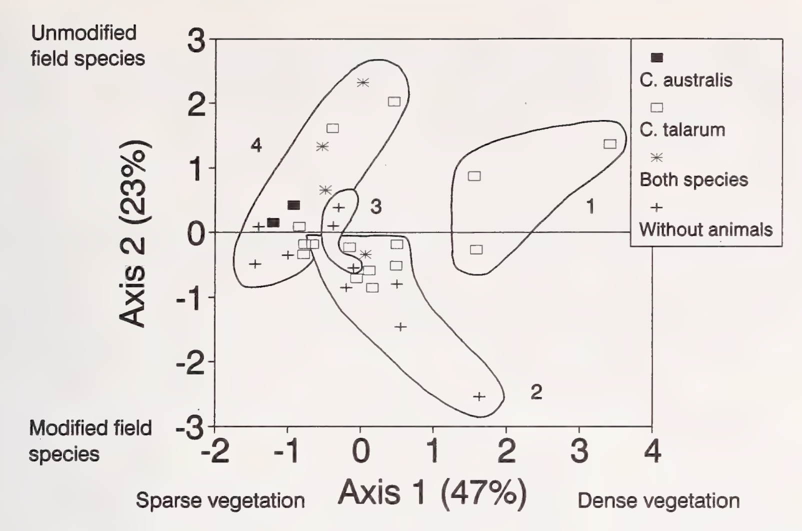


Fig. 2. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Autumn analysis. Values in brackets show the percentage of the variance explained by each axis. Symbols indicate presence of *C. australis, C. talarum*, or both species, respectively. Samples were grouped according to a CA on the referred matrix

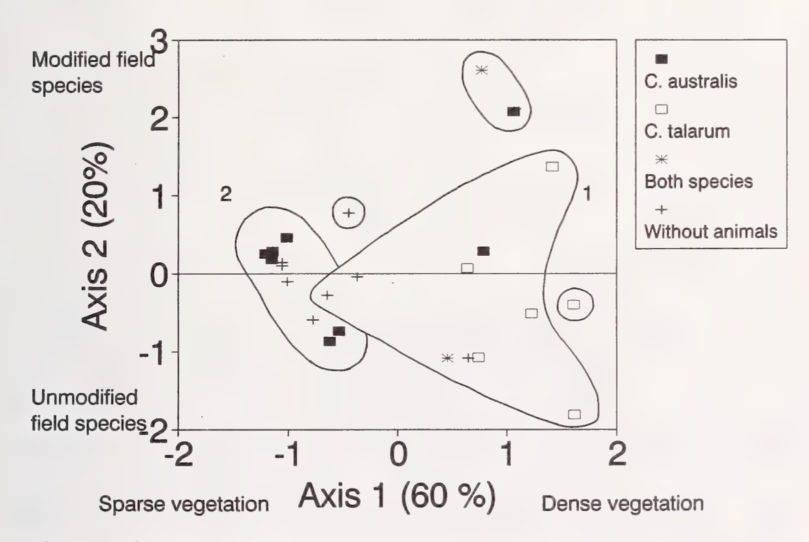


Fig. 3. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Spring analysis. Values in brackets show the percentage of the variance explained by each axis. Symbols indicate presence of *C. australis, C. talarum*, or both species, respectively. Samples were grouped according to a CA on the referred matrix

consequence of some characteristics that are atypical or not relevant in the present context.

In spring, the total number of animals was significantly correlated ($P < 0.05$) with dense vegetation samples, and in autumn with samples that had greater abundance of grasses, perennials, presence of reserve organs and creeping habit. In summer and winter, no significant correlation was found between the total number of animals and vegetation characteristics.

In spring and winter, the distribution of *C. talarum* is more restricted to dense vegetation areas (the number of *C. talarum* individuals showed a significant correlation with position of samples along axis 1, $P < 0.05$), while in autumn and summer its distribution is more dispersed. On the contrary, the distribution of *C. australis* is more restrained in autumn (the number of *C. australis* individuals showed a significant correlation with the position of samples that have greater abundance of grasses, perennials, plants with reserve organs and creeping habit, $P < 0.05$) and in summer (significant correlation with the position of samples that have greater abundance of forbs, glabrous plants, and plants with pivotal roots, $P < 0.05$), while in spring and winter its distribution shows a greater dispersion.

In Figure 4, animal species and animal category distribution was superimposed on to sample distribution along axes 1 and 2 of the PCA on the autumn sample/attribute matrix

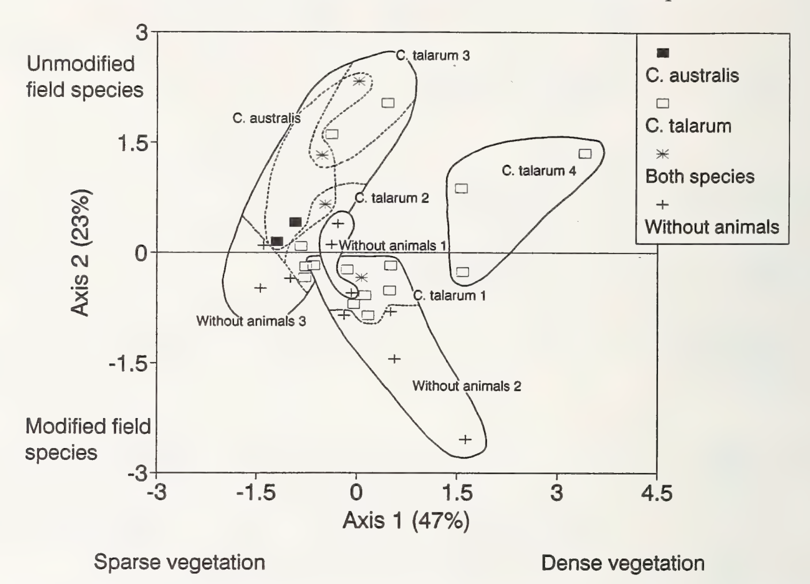


Fig. 4. Ordination of vegetation samples along the first two axes of the PCA of the sample/attributes matrix: Autumn analysis and its relation with animal species and categories. Values in brackets show the percentage of the variance explained by each axis. Samples were grouped according to a CA on the referred matrix. When a vegetation sample group had several animal categories, subdivisions with dotted lines were made. *C. australis* group: 100 % adults; 20 % males; Adult mean weight = 337 g ± 61; *C. talarum* 1: 67 % adults (60 % males); 33 % juveniles (100 % females); Adult mean weight = 119 g ± 21; *C. talarum* 2: 67 % adults (100 % males); 33 % juveniles (100 % females); Adult mean weight = 122 g ± 17; *C. talarum* 3: 80 % adults (100 % males); 20 % juveniles (100 % females); Adult mean weight = 128 g ± 20; *C. talarum* 4: 83 % adults (60 % males); 17 % juveniles (100 % females); Adult mean body weight = 117 g ± 26

(Fig. 2). The spatial distribution of the different animal categories was associated with the existence of vegetation sample groups. Four sample groups with the presence of *C. talarum*, one group with the presence of *C. australis*, and three groups without animals, were defined (Fig. 4). A decrease in the percentage of juveniles and an increase in the percentage of males, was observed through groups 1 to 3 of *C. talarum*. *C. talarum* adult females are only found in groups 1 and 4, whose vegetation presents the greater differences to those of the *C. australis* group. Samples with the presence of *C. australis* and *C. talarum* group 3, which is included in the *C. australis* area, practically do not have annual species, with pivotal roots, present in modified fields. A vegetation gradient is observed through *C.*

talarum groups 1, 2 and 3, where grasses, perennials, plants with reserve organs and creeping habit, become increasingly abundant. This association between animal categories and vegetation was not observed in the remaining seasons.

Discussion

The principal tendency in annual and seasonal data variability shows a contrast between sparse and dense vegetation, as Comparatore et al. (1991) observed in an allopatric population of *C. talarum* in a natural grassland in Mar de Cobo district (Buenos Aires Province, Argentina). In the annual analysis, the positive correlation ($P < 0.05$) between the total number of animals and the position of samples along axis 1 (dense vegetation) could be due to the greater number of *C. talarum* individuals studied (78 animals) compared to *C. australis* (38 animals). This difference is related to the greater density of the *C. talarum* population in the study site than that of *C. australis*, as noted previously. The results indicate that *C. australis* generally concentrates in zones with sparse vegetation, while *C. talarum*, although present in zones with sparse vegetation, concentrates in those with dense vegetation (Fig. 1). Sparse vegetation is associated with sandy and deep soils, having low water retention, while dense vegetation is associated with compact and shallow soils, having higher water retention than the former. These results confirm the hypothesis that subterranean rodent populations can coexist in sympatry by separating niches. This confirms Contreras and Reig's (1965) observations on the same species.

Moreover, the studied sympatric populations greatly differ in their corporal sizes. *C. talarum* adult weight is three times smaller than that of *C. australis* (Malizia et al. in press). Similarly, McNab (1966) observed the greater sized species of pocket gopher has narrower soil tolerances, requiring looser and deeper soils. The smaller species can occupy sandy and deep soils in areas where the larger species is not found, but if the latter one is present, the former would be displaced to marginal and shallower soils. The correlation between the pocket gopher body size and soil texture may be the consequence of a negative correlation between body size and burrow temperature, and therefore be related to thermoregulatory adaptations (McNab 1966). On the contrary, Vleck (1979) based this correlation on energetic adaptations. Nevertheless, McNab's (1966) and Vleck's (1979) explanations are not mutually exclusive. Best (1973) studied the ecology and distribution of three genera of pocket gophers and found the largest species presented the most limited distribution and the broadest range of soil types. The obtained results suggest *C. talarum* has no environmental limitations to occupy typical areas of *C. australis*. When the latter is absent, the spatial occupation of *C. talarum* would be more general. Studying an allopatric population of *C. talarum* in Mar de Cobo district, Buenos Aires Province, Argentina (Comparatore et al. 1991), animals occupied soils with hardness varying from 7 to 52 kg/cm^2. On the contrary, *C. australis* has physiological constraints (Busch 1989), due to its greater body size, which impede the occupation by this species of the typical *C. talarum* area.

Vegetation characteristics, where animal species were studied, vary throughout the year. Animal spatial distribution toward the end of spring, is related to the density of vegetation, and toward the end of autumn to the presence of grasses, perennials, presence of reserve organs and creeping habit. This suggests that toward the end of autumn, when vegetation aerial productivity is low, the animals tend to construct feeding tunnels toward areas where the mentioned attributes characterize the vegetation. Most of these plants are green at this time of the year. The results indicate that animals avoid areas with an abundance of annuals, plants with pivotal roots, plants present in modified fields and forbs, which are dry at this time of the year. Conversely, in spring, when vegetation aerial productivity is high, animals prefer areas with dense vegetation with much green material available. Furthermore, in autumn and winter, as a consequence of the lower availability of

aerial biomass, it would be expected that the percentage of vegetation in the subterranean fraction of animal diets would be greater than in spring and summer. This is in accordance with our results on diet preferences of these animals.

In autumn and summer, distribution of *C. talarum* shows greater dispersion. In contrast, distribution of *C. australis* shows a greater dispersion in spring and winter. These results could be related to the density peaks of each species (MALIZIA et al. in press), the density peak of *C. talarum* being in May–June (autumn, where its occurrence is less restricted) and that of *C. australis* in November–December (spring, also coincident with its less restricted distribution).

Results of summer animal capture (MALIZIA et al. in press) were unexpected as far as the type of soil was concerned, since only in this season was *C. talarum* captured in sandy soils. The scarcity of *C. australis* in the summer study site could be explained by the existence of a compact soil barrier that limited its ingress from sandy soil areas where this species was present in high density. In this condition, *C. talarum* occupied both its typical area and that of *C. australis*. This supports what was stated above that the distribution of *C. talarum* is not limited by soil hardness in this area.

In autumn, it could be observed that animal category distribution (juveniles, females, males) varies concomitantly with the vegetation gradient. No similar relationship was detected for other seasons, thus suggesting that during certain periods of the year other factors, such as social behavior or predation, may be stronger determinants of animal distribution.

In conclusion, these sympatric species occupy area of differing types of soil and vegetation. *C. australis* inhabits areas with sparse vegetation, sandy and deep soils, while *C. talarum* inhabits zones with dense vegetation, and compact and shallow soils. Seasonally, *C. australis* and *C. talarum* show a complementation in their spatial distribution. *C. australis* has a greater dispersion in spring and winter, and a greater restriction in summer and autumn. *C. talarum* has a greater dispersion in summer and autumn, and a greater restriction in spring and winter. "Tuco-tucos" are also associated with fine grain variables as observed in autumn, where the total number of animals, and the number of *C. australis* individuals, were positively correlated with the samples that had abundance of grasses, perennials, plants with reserve organs and creeping habit plants. The data suggest that other factors, such as social behavior or predation, may play an important role in animal spatial distribution.

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Zusammenfassung

Habitatbeziehungen bei sympatrisch lebenden Populationen von Ctenomys australis und Ctenomys talarum (Rodentia, Octodontidae) in natürlichem Grasland

Untersucht wurde die Raumverteilung zweier sympatrisch lebender Populationen von Tukotukos (*C. australis* und *C. talarum*) in Abhängigkeit von Umgebungsveränderlichen in der Nähe von Necochea in der Provinz Buenos Aires, Argentinien. Beide Tierarten leben in Gebieten mit verschiedenen Boden- und Vegetationsarten. *C. australis* bewohnt Gebiete mit wenig Vegetation und sandigem, tiefen Boden, während *C. talarum* Gebiete mit dichter Vegetation und kompaktem, flachgrundigem Boden bewohnt. Die Tukotuko-Populationen wurden auch in Bezug auf andere Variable untersucht: Es wurde im Herbst beobachtet, daß die Anzahl von Tukotukos, insbesondere *C. australis*, positiv mit folgenden Variablen korreliert war: Häufigkeit von Gräsern, ganzjährigen Pflanzen, Pflanzen mit Reserveorganen und von am Boden entlangwachsenden Pflanzen.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Nachweis der Alpenspitzmaus *Sorex alpinus* (Schinz, 1837) im Naturschutzgebiet Seeholz am Ammersee

Von BIRGITT KLETTENHEIMER und M. SALAMON

Eingang des Ms. 26. 8. 1991
Annahme des Ms. 26. 9. 1991

Die Alpenspitzmaus (*Sorex alpinus*) gilt als montanes Element und stellt gleichzeitig ein präglaziales Relikt in europäischen Gebirgen dar. Wie bereits durch einige Funde bestätigt (KAHMANN 1952; SPITZENBERGER 1978), kann die Alpenspitzmaus an günstigen klimatischen Standorten auch in tieferen Lagen (200–500 m) vorkommen. Diese Populationen stellen jedoch von den montan-alpinen Vorkommen der Alpen nahezu getrennte Vorkommen dar.

Im bayerischen Voralpenland konnte die Alpenspitzmaus bisher nur im Bereich von Kochel (605 m ü. NN) und von Unterjoch (1013 m u. NN) (KAHMANN 1952) nachgewiesen werden. Diese Funde bilden die nördlichen Randpunkte des heutigen Verbreitungskerns.

Nördlich dieses Verbreitungskerns sind vermutlich voneinander isolierte Vorkommen im Schwarzwald (LÖHRL 1936), im Harz (SCHULZE 1887; HAENSEL und WALTHER 1969), in der Schwäbischen Alb (LÖHRL 1969), in der Rhön (PIEPER 1973; FELTEN 1984), im Fichtelgebirge (KAHMANN 1952) sowie in der Oberlausitz (ANSORGE und FRANKE 1981) bekannt.

Das Naturschutzgebiet Seeholz (553 m ü. NN) umfaßt ein 97 ha großes Gebiet am Westufer des Ammersees im Landkreis Landsberg am Lech. Auf den Tonablagerungen des spätwürmeiszeitlichen Sees ist ein Eichen-Hainbuchen-Wald vorherrschend, der seewärts in Weiden-Uferwald übergeht. In Senken und feuchten Dellen finden sich auch krautreiche Erlen und Erlen-Eschen-Bestände. Zwei streckenweise sehr stark mäandrierende Bäche mit abgeschnittenen Bachschlingen bilden eine Anzahl von Altarmtümpeln.

In diesem Gebiet wiesen wir im August 1990 im Rahmen einer Kleinsäugererhebung die Alpenspitzmaus (*Sorex alpinus*) nach.

Bei dem gefangenen Individuum handelte es sich um ein adultes Männchen mit einem Körpergewicht von 6 g. Körpermaße: KR-Länge 75 mm, Schw.-Länge 60 mm, HF-Länge 14,3 mm. Am Schädel und am Unterkiefer wurden folgende Maße abgenommen (Meßstrecken nach KAHMANN und VESMANIS 1974): Condylobasal-Länge 18,55 mm, Schädelkapsel-Breite 9,5 mm, obere Zahnreihen-Länge 9,3 mm, maximale Breite über M^2 5,1 mm, Interorbital-Breite 4,5 mm, Condylar-Länge 9,7 mm, untere Zahnreihen-Länge 5,7 mm, Coronar-Höhe 4,3 mm, Postcoronar-Höhe 2,4 mm.

Diese Daten entsprechen den von SPITZENBERGER (1990) durchgeführten Messungen über die Schädelmaße der Populationen der Ostalpen.

Nach SPITZENBERGER (1990) bevorzugt *Sorex alpinus* zwischen 600 und 1700 m langsam fließendes oder sickerndes Wasser und ist dort am häufigsten anzutreffen, wo sich am Bachufer dichte Moospolster bilden. Unter 500 m hingegen ist ihr Vorkommen am ehesten an tief eingeschnittene, schattigkühle Bachschluchten gebunden.

Der Nachweis der Alpenspitzmaus im Naturschutzgebiet Seeholz am Ammersee (553 ü. NN) ist der bislang nördlichste Fund dieser Spezies im Gebiet des Voralpenlandes.

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Vorkommen der Mönchsrobbe *Monachus monachus* auf Sal (Kapverdische Inseln)

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Eingang des Ms. 12. 6. 1991
Annahme des Ms. 26. 9. 1991

Die Mönchsrobbe *Monachus monachus* (Hermann, 1779) bewohnte ursprünglich weite Teile des Mittelmeeres und die südlich anschließende atlantische Küste Nordafrikas bis zum Kap Blanc bzw. bis zum Banc d'Arguin in Mauretanien. Darüber hinaus sind bis in jüngste Zeit Vorkommen von Madeira und den Kanarischen Inseln bekannt. Die Bestände sind heute teils erloschen, teils stark ausgedünnt. Der Gesamtbestand soll weniger als 500 Exemplare umfassen (Marchessaux 1990).

Von den Kapverdischen Inseln war die Mönchsrobbe noch nicht bekannt. Daher erscheint der nachstehende Befund mitteilenswert.

Bei einem Aufenthalt auf der Insel Sal (República de Cabo Verde) fand der Erstautor am 3. 5. 1990 mehrere Skelette von Robben, die vom Zweitautor als der Mönchsrobbe zugehörig determiniert wurden.

Der Fundort liegt im äußersten Südosten von Sal zwischen den Kaps Ponta Jalunca und Ponta Braco de Sirena (Chiffre KI–AF–1990/07). Um eine kleine Bucht sind abwechselnd Sandstrand, Blockgründe und kleine Basaltkliffe mit Grotten gelegen. Im oberen Spülsaum lagen innerhalb einer Küstenstrecke von ca. 500 m mindestens vier verstreute Skelette. Nur von einem Knochenhaufen wurden stichprobenhaft Knochen mitgenommen, die nachträglich zwei wahrscheinlich zusammengehörigen Individuen zugewiesen werden konnten.

Haut und Weichteile fehlten völlig, ebenso eine sichtbare Verfärbung des umgebenden Bodens. Der Bleichungs- und Erhaltungszustand ließ ebenso auf längere Exposition schließen. Wahrscheinlich waren die Tiere im Spätsommer oder Frühherbst 1989 verendet, vermutlich bald nach der Wurfzeit.

Mit einer nahebei gelegenen Fundstätte fossiler Vögel (Boessneck und Kinzelbach 1992) besteht offensichtlich kein zeitlicher oder sachlicher Zusammenhang.

Entnommen wurden insgesamt 12–13 Knochenstücke, die mindestens zwei Tieren zugehören, einem erwachsenen und einem sehr jungen Tier. Adult: 5 Hirnschädelstücke und 1 Nasenbeinpaar. Infantil: 1 Ulna-Corpus und 1 proximales Radiusende, 2 Rippen und 1 ventrales Rippenende, 1 Wirbelkörper (dessen Artbestimmung unsicher ist). Eine Zuordnung zu Sub-Populationen nach van Bree (1978) war noch nicht möglich.

Die Belegstücke befinden sich in der Sammlung des Instituts für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin an der Universität München.

Die Knochen wurden an der Oberfläche im oberen (Winter-)Spülsaum zusammen mit anderem rezenten Anwurf gefunden. Ihr Erhaltungszustand läßt auf eine Exposition über ein Winterhalbjahr hinweg schließen. Bei wesentlich höherem Alter wären sie unter der starken Einwirkung von Sonne, Sandtreiben und Gischt stärker zerfallen und verstreut gewesen. Dies und die potentielle Zuweisung eng beisammen liegender Knochen zu einem Mutter- und einem Jungtier weisen darauf hin, daß die Tiere 1989 noch lebten und daß sie wohl nicht von weither als Kadaver angedriftet sind. Sie lagerten möglicherweise nahe der Fundstelle und kamen hier oder unweit der Fundstelle im Meer zu Tode.

Für die Existenz von Robben auf Sal in jüngerer Zeit spricht der Umstand, daß ein mit

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Abbildungen nach Tieren befragter einheimischer Fischer Robben kannte; angeblich hatte er sie jedoch schon lange nicht mehr gesehen. Weiterhin bezieht sich der Name des benachbarten Kaps „Ponta Braco de Sirena" („Kap der Sirenengrotte") vielleicht auf die Mönchsrobbe, da „sirena" regional auf Robben angewendet wird. Weiterhin gibt es folgende Angabe in MATTHEWS (1989, S. 253): „Manchmal werden (von Sal) kurze Törns nach Boa Vista unternommen, bei denen es nicht ungewöhnlich ist, Tümmler, große Robben und Thunfische zu sehen." Leider konnte der Autor noch nicht näher nach seinen Beobachtungen befragt werden.

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BEKANNTMACHUNG

Einladung

Die 66. Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. findet vom Sonntag, den 20. September, bis Donnerstag, den 24. September 1992, in Karlsruhe statt. Gastgeber ist das Staatliche Museum für Naturkunde.

Vorläufiges Programm

Tag	Zeit	Programm
Sonntag, 20. September:	Anreise	
		Vorstandssitzung
	ab 19.00 Uhr:	Zwangsloser Begrüßungsabend im Restaurant des Schloßhotels, Bahnhofsplatz 2
Montag, 21. September:	9.00 Uhr:	Hörsaal der Badischen Landesbibliothek, Erbprinzenstraße 15 Grußworte und Eröffnung der Tagung durch den 1. Vorsitzenden
	9.30 Uhr:	Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Paläontologie der Säugetiere“
	14.00 Uhr:	Posterdemonstration im Staatlichen Museum für Naturkunde, Erbprinzenstraße 13
	15.00 Uhr:	Kurzvorträge im Hörsaal Landesbibliothek
	17.00 Uhr:	Mitgliederversammlung
	20.00 Uhr:	Empfang durch die Stadt Karlsruhe im Rathaus, Marktplatz
Dienstag, 22. September:	9.00 Uhr:	Hörsaal Landesbibliothek: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Sozialverhalten der Säugetiere“
	14.30 Uhr:	Kurzvorträge
	16.30 Uhr:	Posterdemonstration im Museum
	19.00 Uhr:	Führung durch das Museum
	20.00 Uhr:	Filmabend im Museum
Mittwoch, 23. September:	9.00 Uhr:	Hörsaal Landesbibliothek: Hauptvortrag und Kurzvorträge zum Themenschwerpunkt „Chiroptera“
	14.30 Uhr:	Kurzvorträge
	15.45 Uhr:	Posterprämierung und Abschluß des wissenschaftlichen Programms
	16.30 Uhr:	Führung durch den Zoo Karlsruhe
	20.00 Uhr:	Geselliger Abend im Staatlichen Museum für Naturkunde
Donnerstag, 24. September:		Exkursion zu den Mooren an der Hornisgrinde im Nord-Schwarzwald
Freitag, 25. September:		Arbeitstreffen verschiedener Arbeitsgemeinschaften

Alle Interessenten sind zu dieser Tagung herzlich eingeladen. Falls eine persönliche Einladung gewünscht wird, wenden Sie sich bitte an den 1. Vorsitzenden, Prof. Dr. U. Schmidt, Zoologisches Institut, Poppelsdorfer Schloß, W-5300 Bonn 1 (Tel. 02 28/ 73 54 68; Fax-Nr. 02 28/73 54 58).

Das Programm mit der Vortragsfolge wird den Mitgliedern – auf Anforderung auch Nichtmitgliedern – rechtzeitig vor der Tagung zugesandt. Außer Beiträgen zu den genannten Themenschwerpunkten werden auch dieses Mal wieder Vorträge und Posterdemonstrationen zu anderen Fachgebieten der Säugetierkunde berücksichtigt. Bitte melden Sie Kurzvorträge (15 Min.) und Posterdemonstrationen möglichst frühzeitig, spätestens jedoch bis zum 30. April (Ausschlußfrist) beim Geschäftsführer unserer Gesellschaft, Prof. Dr. H. Erkert, Zoologisches Institut, Auf der Morgenstelle 28, W-7400 Tübingen (Tel. 0 70 71/29 29 58; Fax: 0 70 71/29 46 34) an.

Mit Fragen zum Tagungsort und zur Organisation wenden Sie sich bitte an Herrn Dr. R. Flösser, Staatliches Museum für Naturkunde Karlsruhe, Postfach 6209, W-7500 Karlsruhe 1 (Tel. 07 21/17 51 65; Fax: 07 21/17 51 10).

BUCHBESPRECHUNGEN

McFarland, D.: **Biologie des Verhaltens.** Evolution, Physiologie, Psychobiologie. Hrsg. A. Stahnke und K. Vogler. Deutsch von W. Dressen, V. Laske und B. Nixdorf. 531 S., 357 Abb., 12 Tab. Weinheim: VCH Verlag 1989. DM 78,–. ISBN 3-527-26479-5

Dieses Buch ist eine überarbeitete und erweiterte Übersetzung der Originalfassung „Animal Behaviour" von 1985. Es soll die Ergebnisse der Verhaltensforschung übersichtlich darlegen und Studenten der Biologie und auch der Psychologie zur Einführung und als Studienbegleiter dienen. Vorrangiges Anliegen des Autoren ist dabei, zwischen diesen beiden Wissenschaften eine Brücke zu schlagen und moderne, in der evolutiven Entfaltung der Arten begründete Denkansätze der vergleichenden Ethologie darzustellen.

Im Anschluß an eine kurze Einführung in die Verhaltensforschung ist der Stoff in 3 Teile mit jeweils wiederum 3 zugeordneten Kapiteln in unterschiedlich gewichtete Abschnitte gegliedert. Die Hauptteile und Kapitel sind wie folgt überschrieben: 1. Evolution des Verhaltens (Genetik und Verhalten; natürliche Selektion; Evolution und Sozialverhalten), 2. Mechanismen des Verhaltens (Wahrnehmung bei Tieren; das Tier und seine Umgebung; Lernen), 3. Komplexes Verhalten (Instinkt; Entscheidungsfindung bei Tieren; die kognitiven Fähigkeiten der Tiere). Den 9 Kapiteln vorangestellt sind kurze Einleitungen, in denen die Bedeutung folgender Persönlichkeiten für die entsprechenden Wissenschaftsbereiche geschildert wird: G. Mendel, Ch. Darwin, R. Fisher; J. P. von Müller, C. Bernard, I. Pawlow; K. Lorenz und N. Tinbergen, K. von Frisch, E. Tolman. Das Buch ist mit vielen Abbildungen illustriert und von ansprechender großformatiger Aufmachung.

Dieses Konzept der Themenzusammenstellung ist neu und abweichend von anderen deutschsprachigen Lehrbüchern. Viele Erkenntnisse der allgemeinen und speziellen Zoologie sind integriert und dienen zur Erklärung vor allem funktioneller Zusammenhänge. Aus der möglicherweise etwas konservativen Sicht des Rezensenten ergeben sich jedoch erhebliche Zweifel, nicht an der Bedeutung der Ethologie als eine zoologische Forschungsrichtung, sondern vielmehr an der Art der Darstellung biologischer Phänomene und der häufig sehr einseitigen, vor allem wenig kritischen und teleologischen Interpretation evolutiver Prozesse. So kann die Aussage im Geleitwort, daß hier die fleißige Schar der Bearbeiter Hervorragendes geleistet hat und daß mit fachlicher Umsicht ein auch sprachlich erfreuliches Werk geschaffen wurde, nicht nachvollzogen werden. Das Buch zeigt viele ungeschickte, über zweifel- bis zu fehlerhaften Formulierungen. In dieser Hinsicht veranlaßt der deutsche Titel bereits zum Nachdenken, aber es ist auch von „Elternfürsorge" (gemeint ist parental care), von „Sinnesökologie", von „ungünstigen Lebensräumen" und von „instrumentellem Lernen" allein in den Überschriften die Rede. Die sprachlichen Formulierungen sind besonders in jenen Schilderungen störend, in denen kausale und nach menschlichen Bewertungen anzustrebende, sinnvolle Entwicklungszwänge unterstellt werden. Das unglücklicherweise weit verbreitete Wort Strategie gewinnt in seiner ursprünglichen Bedeutung unterschwellig an Gewicht, obwohl eingangs mehr im Sinne einer genetisch bedingten, selektionsabhängigen Adaptation definiert.

Die sachliche Information ist – zumindest in weiten Teilen des Buches – ebenfalls geeignet, Verwirrung auszulösen. Sie ist weder konzentriert noch komprimiert, eher ungeordnet, stellenweise stark simplifiziert und falsch. Viele triviale und banale Aussagen, zahlreiche Widersprüche, Wiederholungen, Abweichungen von der Thematik und langatmig geschilderte, einseitig bewertete Paradebeispiele der Ethologie wechseln einander ab. Viel theoretischer und abstrakter Balast betont die Bedeutung der Verhaltensforschung. Über taxonomische Regeln wird hinweggesehen, indem häufig Arten mit Gattungsnamen ausgewiesen und deutsche Bezeichnungen für Arten entweder ungebräuchlich oder falsch sind. Der Leser lernt ferner eine „Äquifinalität" kennen, jedoch nicht den Unterschied zur Konvergenz; die „natürliche Auslese wirkt auf die physischen Eigenschaften (den Phänotyp) eines Individuums, zu denen auch sein Verhalten gehört", (bleibt der Genotyp verschont?); auf S. 28 ist Lernen vor Schlupf bzw. Geburt nicht möglich, auf S. 30 hingegen doch: „Dreizehenmöwen haben viele feindvermeidende Anpassungen anderer Möwen verloren"; eine „evolutionäre Strategie" ist eine „Verhaltensanweisung, die im Laufe der Evolution entwickelt wurde"; Ähnlichkeiten von Tieren mit Teilen von Vegetation oder von anderen Tieren sind eine „Verhaltensweise, mit denen Tiere versuchen, ihre Feinde abzuwehren"; auf S. 140 ist das menschliche Gehirn „viermal so groß, wie es bei Primaten von ähnlicher Statur zu erwarten wäre", auf S. 168 nur noch dreimal; „Sinnesrezeptoren sind spezialisierte Nervenzellen" mit „einem oder mehreren Axonen"; eine Verkürzung des Muskels ist nur dann möglich, wenn er an beiden Endpunkten nicht fixiert ist; „Protozoen können kein echtes Nervensystem ausbilden" (was ist ein unechtes und warum sollten sie?); Plathelminthen haben ein Strickleiternervensystem; „zum extrapyramidalen System zählen alle nicht-reflexartigen motorischen Bahnen, die weder im cortico-spinalen noch im pyramidalen System integriert sind"; in der „Reihenfolge Fisch, Reptil, Vogel, Säuger" gibt es „keine fortschreitende Gehirnvergrößerung", etc. Eine Konzentration von trivialen und falschen Aussagen wird auf S. 181 erreicht: „Nicht bei allen Vertebraten sind die Ohren gleich gebaut. So haben etwa Fische und Wale kein äußeres Ohr. Fische haben auch kein Mittelohr mit Trommelfell und Gehörknöchelchen. Da das Gewebe der Fische eine

ähnliche Dichte wie Wasser hat, können Vibrationen, die am Kopf eintreffen, direkt zum Innenohr weitergeleitet werden. Einige Fische verfügen allerdings über einen Mechanismus, der ähnliche Funktionen erfüllt wie die des Innenohrs. Hierbei handelt es sich um die luftgefüllte Schwimmblase, die durch eine knöcherne Verbindung zum Innenohr das Hörvermögen gewaltig verbessert. Bei Amphibien und Reptilien bildet das Trommelfell den äußeren Teil des Ohres. Bei Vögeln gibt es einen Gehörgang (Meatus acusticus), der von der Körperoberfläche zum Trommelfell führt. Ein stäbchenähnlicher Knochen, die Columella, stellt hier eine Verbindung zur Innenoberfläche des Trommelfells her und tritt mit dem Steigbügel in Kontakt. Bei den Amphibien und Reptilien bilden diese Knochen Teile des Kiefers, obwohl bei einigen Arten diese Knochen auch Hörfunktionen ausüben." Dem Abschnitt über das Vertebratengehirn und den Beiträgen über Intelligenz und Hirngröße hätte mehr Sorgfalt nach gründlicherem Literaturstudium gutgetan. Viele Abbildungen sind überflüssig, da sie nicht zum Verständnis des Textes beitragen.

Der Versuch, Erkenntnisse aus Genetik, Anatomie, Physiologie und Ökologie unter ethologischen Aspekten zu subsummieren, ist nicht gelungen. Wenn dieses eine Standortbestimmung der modernen Ethologie sein soll, dann wurde dieser Disziplin ein schlechter Dienst erwiesen, keine gute „Strategie".

D. Kruska, Kiel

RÖHRS, M.; MEYER, H. (Hrsg.): **Studium Generale.** Vorträge zum Thema „Mensch und Tier". Bd. VII. Hannover: M. u. H. Schaper 1990. 105 S. DM 19.50. ISBN 3-7944-0162-X

Der vorliegende 7. Band der Serie „Mensch und Tier" enthält die Vorträge zum Studium Generale, Hannover im WS 88/89. GRUNERT behandelt das Thema „Geburt und Geburtshilfe" vergleichend beim Menschen aus historischer und ethnographischer Sicht und bei Säugetieren in ganzer Variationsbreite. BISPING gibt eine Übersicht zum Thema „Seuchen und Geschichte", vor allem über die großen Seuchenzüge von Fleckfieber und Pest, und zeigt deren Einflüsse auf Kultur, Lebensweise und historisches Geschehen auf. Gleichzeitig wird aber auch darauf hingewiesen, daß der Mensch durch rasche Änderungen der Lebensweise Auftreten und Ablauf der Seuchen beeinflußt hat. H. MEYER bringt mit seinem Beitrag „10 000 Jahre Schwein gehabt" einen lesenswerten Beitrag zur Kulturgeschichte des Hausschweins, seine Herkunft und Bedeutung in Mythos, Sage und Religion. FRANKE berichtet anhand zahlreicher Abbildungen über Tierbilder auf antiken Münzen mit ausführlichem Kommentar. OHLY legt eine umfangreiche, weit ins Detail reichende Abhandlung über WOLFRAMS Parsival vor, die eine umfassende Analyse des Pferdebildes im Hochmittelalter bringt und damit zugleich einen wesentlichen Beitrag zum Menschenbild liefert. Die differenzierte Bewertung des Pferdes in jener noch autofreien Zeit – auch als Imponierapparat für seinen Besitzer – ist beachtlich. Die Veröffentlichung wendet sich an einen größeren Interessentenkreis und kann empfohlen werden. Zahlreiche Abbildungen illustrieren die meisten Beiträge.

D. Starck, Frankfurt/M.

REICHERT, H.: **Neurobiologie.** Stuttgart,New York: Georg Thieme Verlag 1990. 391 S. DM 46,–. ISBN 3 13 745301 1

Die Neurobiologie hat sich zu einem eigenständigen Fach entwickelt. In 9 Kapiteln versucht das Taschenbuch eine kurze Übersicht über Probleme, Methoden und Ergebnisse dieses Forschungszweigs zu geben. Neben einer Darstellung von Struktur, Ontogenese sowie Erhaltung und Reparaturvorgängen an Nervensystemen steht die Besprechung der Funktion des Neurons, der Synapse und der Neuronenverbände mit ihren Teilsystemen (Motorik, Sensorik, Integration) im Mittelpunkt. Das Abschlußkapitel befaßt sich mit der Frage von Plastizität und Lernvorgängen.

Dem Kapitel zur vergleichenden Morphologie der Nervensysteme (Kapitel 1) würde man mehr Raum wünschen, damit auch ein Bezug zu aktuellen Forschungsergebnissen möglich ist. Auch die Auseinandersetzung mit dem Problem „Lernen" (Kapitel 9) hätte es verdient, stärker vertieft zu werden, handelt es sich doch hier um ein zentrales Problem der Neurobiologie, an dem intensiv gearbeitet wird. Diesen kritischen Punkten steht der größere Teil des Buches entgegen, der zunächst die zelluläre und molekulare Ebene der Neurobiologie aufarbeitet und dabei gleichermaßen Struktur und Funktion berücksichtigt. Hier wird eine gute Basis geschaffen, auch der aktuellen Forschung zu folgen. Die breite Darstellung der Leistungen des Nervensystems in systemhaften Zusammenhängen verbindet dann eine Fülle von Sachinformationen mit der Präsentation einer Forschungsstrategie, die für die aktuelle Neurobiologie so typisch ist. Eine didaktisch geschickte Darstellung mit klaren und aussagekräftigen Abbildungen und einem gut strukturierten Text steigert die Attraktivität des Taschenbuches, dessen hoher Preis den Weg zu der erklärten Zielgruppe (Studierende) allerdings nicht leichter machen wird.

G. Rehkämper,Köln

Dittrich, L.; Rieke-Müller, A.: **Ein Garten für Menschen und Tiere.** 125 Jahre Zoo Hannover. Hannover: Verlagsgesellschaft Grütter 1990. Format 24,5 × 29,5 cm, 228 S., über 200 Abb. DM 49,80. ISBN 3-9801063-2-2

Der Band wurde zum 125jährigen Bestehen des Zoologischen Gartens Hannover von seinem wissenschaftlichen Leiter, L. Dittrich, und der Historikerin A. Rieke-Müller gemeinsam verfaßt. Er schildert das wechselvolle Schicksal dieser Einrichtung, der von ihr verfolgten Ziele und die den Garten in Anlage und Bauten, Auswahl, Haltung und Präsentation der Tiere prägenden Anschauungen.

1860 geplant, wurde der Zoo von einem Aktionärsverein mit Unterstützung der Stadt Hannover ins Leben gerufen und 1865 eröffnet. Die wertvollsten Säugetiere der damals enthaltenen etwa 30 Arten waren zwei im Kölner Zoo geborene Löwen, ein Bison, zwei Axishirsche und zwei Schwarzbären. Auch weiße Ratten und eine weiße Maus finden sich auf der Liste, was im Blick auf die Entstehung von Laborratte und -maus von Interesse sein mag. Die Unterkünfte der Tiere waren mehr an romantischen Vorstellungen als an dem Wohlbefinden der Insassen orientiert.

Der Kampf um die Finanzierung unter dem Einfluß von Persönlichkeiten, Parteien, Regierungen und dem Zustand der Wirtschaft steht im Vordergrund. Politische und weltanschauliche Ideen wirken sich ebenso aus wie der Fortschritt in Tiermedizin und Ethologie sowie die zunehmende Gefährdung der Tierwelt in der Natur. Verluste durch Seuchen und Gewinn durch Zucht, Tierfangexpeditionen, Völkerschauen, aber auch die Aussetzung gefährdeter Arten (Arabische Oryx, Mendes-Antilopen) werden behandelt, das „Hannoversche Modell" bei der Reduktion von Gehege-Grenzen wie der Einfluß der Tierhandelsfirma Ruhe. An Beziehungen zu Wilhelm Busch, Hermann Löns und Richard Gerlach erinnert die Festschrift. Über die wichtigsten Persönlichkeiten aus der Gründerzeit findet man kurze biographische Abschnitte.

Aus allem ist eine vielseitige, bunt illustrierte Zoogeschichte entstanden, die mit zahlreichen Literaturhinweisen und Anmerkungen belegt wird. Der Zoologe würde gern noch mehr über das Auf und Ab im Tierbestand, über bemerkenswerte Arten, Zuchterfolge oder biologische Arbeiten an den Zootieren erfahren. Zu den oft historisch wichtigen Bildern wären mehr Informationen und vor allem auch Quellenangaben erwünscht gewesen. Das Farbbild S. 168 macht seine schwarzweiße Reproduktion S. 150 eigentlich überflüssig.

Dennoch ist die vorliegende Zoogeschichte nicht nur für den Besucher und Kenner des Zoos Hannover eine inhaltsreiche und unterhaltsame Lektüre. Als Musterbeispiel für die Geschichte zoologischer Gärten ist sie von allgemeinem Interesse. J. Niethammer, Bonn

Guthrie, R. D.: **Frozen Fauna of the Mammoth Steppe.** The Story of the Blue Babe. Chicago: University of Chicago Press 1990. XIV + 323 pp., numerous figures. US $ 45,95. ISBN 0-226-31123-6

Anlaß zu dieser Publikation war ein etwa 8–9jähriges Bison-„Kalb" (der Name Blue Babe bezieht sich auf die Vivianit-Kristalle auf der Haut), das aus dem Frostboden einer Goldmine in Zentralalaska im Jahre 1979 geborgen wurde. Das radiometrische Alter wird mit ungefähr 36 000 Jahren angegeben, entspricht also einem jungeiszeitlichen Interstadial. Der Verfasser, als Professor für Zoologie an der Universität Alaska ein bekannter Säugetier-Paläontologe, schildert eingehend die Entdeckung und Bedeutung der eiszeitlichen Mammut- (und Nashorn-)Kadaver in Sibirien (vom Beresovka-Mammut bis zum Dima-„Baby") und die vermutlichen Ursachen ihrer Erhaltung sowie der bisherigen Bison- und Elch-„Mumien"funde in Alaska. In den weiteren Kapiteln beschreibt Guthrie nicht nur die erste wissenschaftliche Ausgrabung einer jungeiszeitlichen (Bison-)„Mumie" in Nordamerika, sondern analysiert auch eingehend die Todesursachen des Jung-Bison (durch Löwen im frühen Winter), die einstige Umwelt der Mammut-Steppe, die als trockene Kaltsteppe gedeutet wird und ferner die Ethologie, Ökologie und Phylogenie der Steppenbisons. Guthrie klassifiziert die nordamerikanischen Steppenbisons als *Bison priscus* (mit Unterarten), wobei das Problem der parallelen Evolution und die stammesgeschichtliche Herkunft von *Bison bison* diskutiert werden. Ein Schlußkapitel ist der Präparation, Rekonstruktion und Montage der Bison-„Mumie" im Museum der Alaska-Universität in Fairbanks gewidmet. Ein Literaturverzeichnis und ein Register vervollständigen die Publikation. Zahlreiche Illustrationen ergänzen den lesenswerten und auch für einen weiteren Leserkreis interessanten Text. Das Buch kann nur bestens empfohlen werden. Etliche Druckfehler werden nur den Fachmann stören. E. Thenius, Wien

Deutsche Gesellschaft für Säugetierkunde: Referate, Vorträge und Posterdemonstrationen der 64. Hauptversammlung 1990

Ein Hauptziel der Deutschen Gesellschaft für Säugetierkunde ist, auf ihren Jahrestagungen über Säugetiere arbeitende Wissenschaftler verschiedenster Fachrichtungen zusammenzuführen, den Gedanken- und Erfahrungsaustausch anzuregen, um so Erkenntnisse aus den einzelnen Forschungsgebieten zu integrieren. Die Kurzfassungen der Vorträge und Posterdemonstrationen von der 64. Hauptversammlung, die in diesem Jahr in Osnabrück stattfand, liegen wiederum als Sonderheft der »Zeitschrift für Säugetierkunde« vor. Die Tagung war durch drei Themenschwerpunkte gekennzeichnet, die ökologische, ontogenetische und ernährungsphysiologische Fragestellungen behandeln. Zusätzlich wurde eine große Zahl freier Beiträge angeboten. Diese auch in der Vergangenheit geübte Art der Themendarbietung soll die Breite der aktuellen Säugetierforschung widerspiegeln. Die säugetierbiologische Arbeit war in der Ethologie von Anfang an ein Forschungsschwerpunkt. Im Vordergrund stehen Projekte mit öko-ethologischer Fragestellung. Da sich dafür stenöke Säugetiere besonders eignen, werden bevorzugt silvicole und ripicole Arten in Gehegen und im Freiland beobachtet. Eine intensive Freilandarbeit, auch auf Exkursionen, förderte die Untersuchung von Kleinsäugetiergemeinschaften. Die Kurzfassungen der Vorträge und Posterdemonstrationen der Deutschen Gesellschaft für Säugetierkunde sind ab der 58. Hauptversammlung 1984 in Göttingen noch lieferbar. Zu beziehen durch jede Buchhandlung. ★ **Deutsche Gesellschaft für Säugetierkunde, 64. Hauptversammlung in Osnabrück, 23. bis 27. September 1990.** Kurzfassungen der Vorträge und Posterdemonstrationen. Herausgegeben von Dr. Christel Schmidt, Bonn, und Prof. Dr. Rüdiger Schröpfer, Osnabrück. 1990. 55 Seiten. Kartoniert 24,– DM

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Erscheinungsweise und Bezugspreis 1992: 6 Hefte bilden einen Band. Jahresabonnement Inland: 358,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 351,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 358,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Rüsse/Sinowatz

Lehrbuch der Embryologie der Haustiere

Von Prof. Dr. med. vet. Imogen Rüsse, Inst. für Tieranatomie, Univ. München, und Prof. Dr. med. vet. Dr. med. Fred Sinowatz, Inst. für Tieranatomie, Univ. München sowie unter Mitarbeit von Prof. Dr. med. vet. Angela von den Driesch, Inst. für Palaeoanatomie, Domestikationsforschung und Geschichte der Tiermedizin, Univ. München. Zeichnungen von Bettina Buresch und Barbara Ruppel, beide München.
Ca. 480 Seiten, 318 Abbildungen mit 710 Einzeldarstellungen, davon 83 farbig sowie 39 Tabellen. Gebunden DM 178,– **ISBN 3-489-57716-7**

Das neue Lehrbuch der Embryologie der Haustiere ist konzipiert als Nachfolgewerk der Entwicklungsgeschichte der Haustiere von Zietzschmann/Krölling. Es umfaßt die embryonale und fetale Entwicklung des Rindes, des Pferdes, des Schweines, der kleinen Wiederkäuer, des Hundes, der Katze und des Vogels, wobei die Entwicklungsstadien von der Befruchtung bis zur Geburt in zeitlicher Folge in ausführlichen Tabellen dargestellt werden. Der frühen Entwicklung des Konzeptus und seinem Kontakt mit dem Muttertier wird besondere Aufmerksamkeit gewidmet, um das Lehrbuch auch für diejenigen interessant zu gestalten, die sich mit den neuen, am Haustier durchgeführten Biotechniken befassen. Besonders ausführliche Kapitel gelten den Themen Gametogenese, weiblicher Sexualzyklus, Befruchtung und Furchung des Eies, Frühgravidität, Implantation und Plazentation. Weitere Abschnitte beschäftigen sich mit der Entwicklung des Nervensystems, der Harn- und Geschlechtsorgane sowie, erläutert am Beispiel des Schafes und der Katze, mit der Entwicklung des Gesichtes. Stets werden dabei die neuesten Erkenntnisse, eigene Forschungsergebnisse der Autoren sowie die einschlägige in- und ausländische Literatur berücksichtigt. Zu der reichhaltigen Bebilderung gehören neugestaltete Zeichnungen ebenso wie Fotos von Präparaten, die eigens am Institut für Tieranatomie hergestellt wurden. Für einen großen Interessentenkreis, Studierende der Veterinärmedizin, Tierärzte, Tierzüchter, Mediziner, Biologen und Embryologen, steht mit diesem neuen Werk nun wieder ein aktuelles, didaktisch modernes Lehrbuch und Arbeitsmittel zur Verfügung.



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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

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The biology of *Pipistrellus bodenheimeri* (Microchiroptera) in the Dead Sea area of Israel

By Y. Yom-Tov, D. Makin, and B. Shalmon

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Receipt of Ms. 4.7. 1991
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Abstract

Collecting data on the biology of *Pipistrellus bodenheimeri* during a survey of the bats of the Dead Sea area. This species is a year-round resident, hibernating between October and April. Capture rate during winter was 5 % of the summer rate. Lactating females were found between early May and early September. Females are significantly heavier and larger than males. The bats feed intensively in the evening and gain about 15 % of body weight within 2 h.

Introduction

Very little work has been carried out on the biology of any bats in the Near East (Atallah 1977–1978; Bates and Harrison 1989; Harrison 1984; Harrison and Makin 1988; Makin 1977; Mendelssohn and Yom-Tov 1988; Qumsiyeh 1965). *Pipistrellus bodenheimeri* was described by Harrison (1960), and it is found from the Dead Sea area to Aden. It is one of the smallest (less than 3 g) and least known species of its genus, and one of the smallest bats in the Palearctic region.

The aim of this study is to report data of the biology of *P. bodenheimeri* which we gathered during a survey conducted in the insectivorous bats of the Dead Sea area (Yom-Tov et al. 1991).

Material and methods

Study area

The study area is the western and southern coastal plain of the Dead Sea, a long (about 80 km) and narrow (about 15 km) salt lake which lies 400 m below sea level. It is a desert area, with mean annual precipitation of 50 mm which falls only during winter (November–April). Mean daily temperatures of 16–18 °C exist in December–February and 32–34 °C during June–August. Mean minimum monthly temperature is reached in January (11 °C) and mean maximal temperature in July (39 °C). Mean monthly relative humidity fluctuates between 35 % (July) and 50 % (January) (climatological data from Jaffe 1988). The coastal plain borders with high cliffs intersected by dry wadi beds. Several small oases and agricultural settlements exist along the valley, providing drinking water for wildlife. The vegetation is savannoid desert vegetation, with *Acacia* trees near and in the wadi beds and low bushes of the plain (Danin 1988).

Survey procedure

The study was conducted between April 1988 and January 1990. We made an effort to visit the area every 3–4 weeks during winter (November–April) and twice monthly during the rest of the year. Most visits lasted one day, but during the first summer there were several two-day visits. During the first summer we sampled various localities along the western shore of the Dead Sea from Ain Fashkha 36°27′ E, 31°44′ N (Occupied areas) in the north through the oasis of En Gedi 35°26′ E, 31°28′ N, and its environs, Nahal Zeelim 35°23′ E, 31°21′ N, En Boqeq 35°23′ E, 31°10′ N, Brechot Navit 35°23′ E, 31°07′ N and south to Neot Hakikar 35°23′ N, 30°55′ N. We caught bats at night using

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monofilament and other mist nets, erected between vegetation and in open areas. We visited several caves, mostly in En Gedi area, but also near en Boqeq and Mt. Sdom 35°23′ N, 31°05′ N and tried to identify bats there by direct observation and by sampling the population by mist nets. We also observed bats near street lights at various settlements along the shore. Several bats were caught by abruptly waving mist nets towards approaching bats near street lights. After the first summer we concentrated most of our efforts in Neot Hakikar, where we repetitively erected mist nets, about 30 m long, parallel to the water line of a 40 m diameter irrigation pond. The nets were kept open from about 30 min before sunset to at least 3 hours after dark (normally 4–6 hours on average each summer night). Every individual captured was identified to its species and sex, its forearm measured by a digital caliper to 0.1 mm accuracy and weighted with Pesola spring balances to 0.1 g accuracy. Age was determined by examining the degree of ossification of the finger joints (KUNZ and ANTHONY 1982). Body condition, pregnancy, lactation and testis size were noted in the animal released on the spot.

Results and discussion

Pipistrellus bodenheimeri was the most commonly found bat in our survey, with a total of more than 250 individuals netted. It was netted or observed every month of the year, but mainly between May and September, indicating that it is a resident species. The rate of capture (average number netted in 30 m net during 3 hrs at the beginning of an evening) in the summer was 20 times that of winter (Fig. 1). At least two possible explanations may account for this result: 1. The bats hibernate between October and April and arousal rate during hibernation is 5 % (1:20), or 2. during winter there are more water sources available, and the bats disperse accordingly. We believe that the first explanation is correct since the number of bats hunting near street lights in winter is smaller by an order of magnitude than that in the summer.

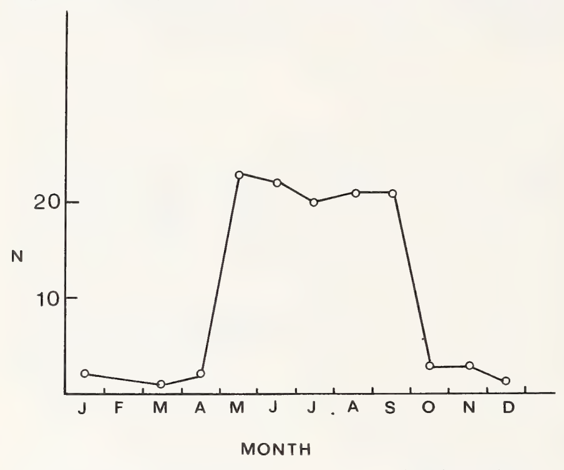


Fig. 1. The average number of *Pipistrellus bodenheimeri* caught during the year in a 30 m long mist net in a 3-hour period at the beginning of an evening in Neot Hakikar

P. bodenheimeri was caught even at ambient temperatures of 11 °C. We did not find a correlation between ambient temperature at the night of netting and either the number of species or the number of individuals caught. Neither there was a correlation between the moon phase and the number of bats caught during the summer (April–October).

Females (n = 143) were significantly ($t = 3.3$; $p < 0.01$) heavier than the males (n = 119; mean body weight 2.9 and 2.5 g, respectively), and had significantly ($t = 3.1$; $p < 0.001$) greater forearm length (mean 30.1 and 29.2 mm, respectively). Mean body weight (but not mean forearm length) fluctuated during the year (Fig. 2), reaching a maximum in May and a minimum in August. The average high body weight in May was probably due to the improved food conditions in spring and the combined effect of this and pregnancy in females. The decline in average body weight towards August was due to the appearance of young bats, which are easily distinguishable from the adults by having greyer fur, especially on the abdomen, and incomplete fusion of the epiphysis in the joints of the fingers. Young bats formed a large proportion (up to 50 %) of the netted sample in July and August. The first young *P. bodenheimeri* were caught on 14 June 1989. These were

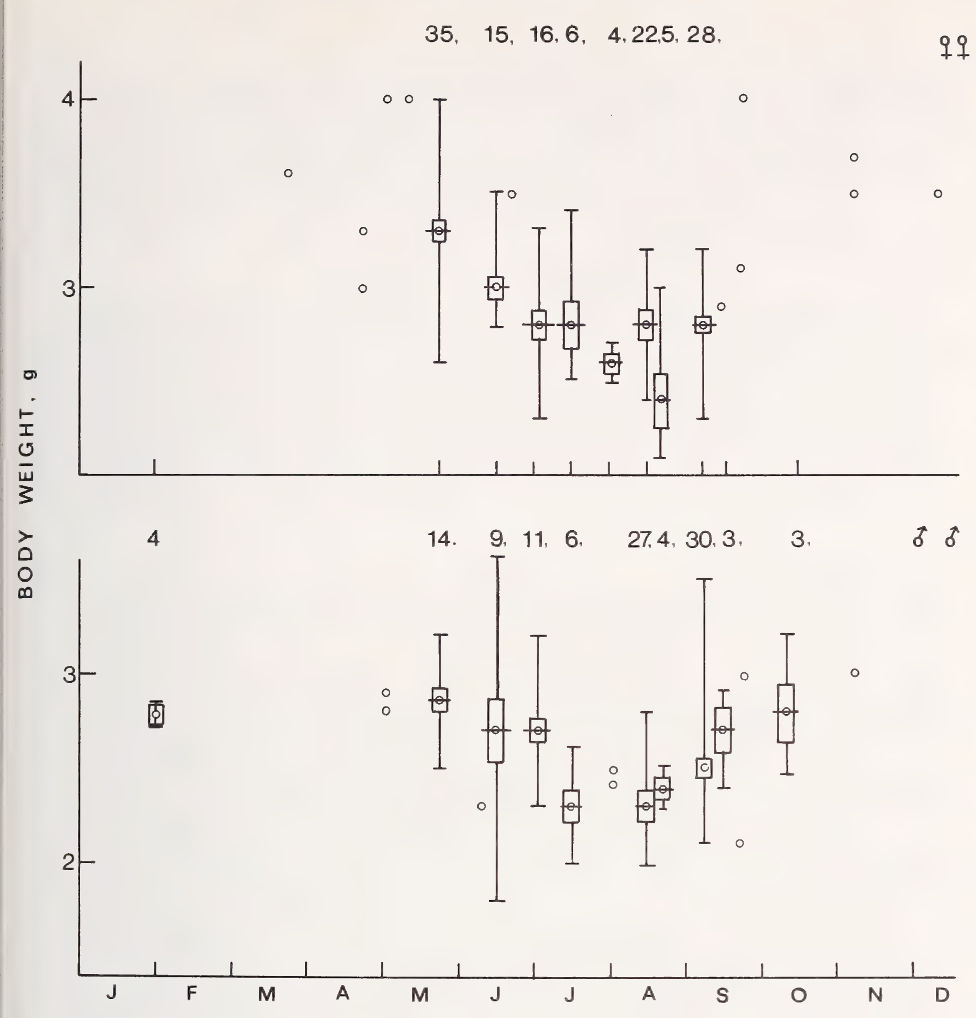


Fig. 2. Body weight (a) of male and female *Pipistrellus bodenheimeri* caught in the Dead Sea area during the year. Means, SE and ranges. Sample sizes for samples larger than three are given above the means

2 females weighing 2.9 and 3.0 g, respectively, with forearms measuring 30.3 and 20.9 mm, respectively; and a male, weighing 1.8 g (the lightest *P. bodenheimeri* ever caught) with a forearm measuring 27.0 mm. These three specimens composed 12.5 % of the 24 captured during that evening, but the percentage of young bats increased to 45 % and 53 % of the samples caught in July and August, respectively. The forearms of the young bats were not significantly different from those of the adults, but body weight was lighter in July. In that month adult males were 21 % heavier than the young ($t = 5.0$, $p < 0.001$, $df = 9$), and adult females were 15 % heavier ($t = 3.8$, $p < 0.01$, $df = 14$). In August the difference decreased and the body weight of young animals was not significantly different from that of the adults.

Lactating females were captured from 24 May until 3 July, but evidence of recent lactation (protruding nipples with no hair 3–5 mm around) was noticed between 2 May until 7 September. Of the 102 females checked during the summer for signs of lactation, 90

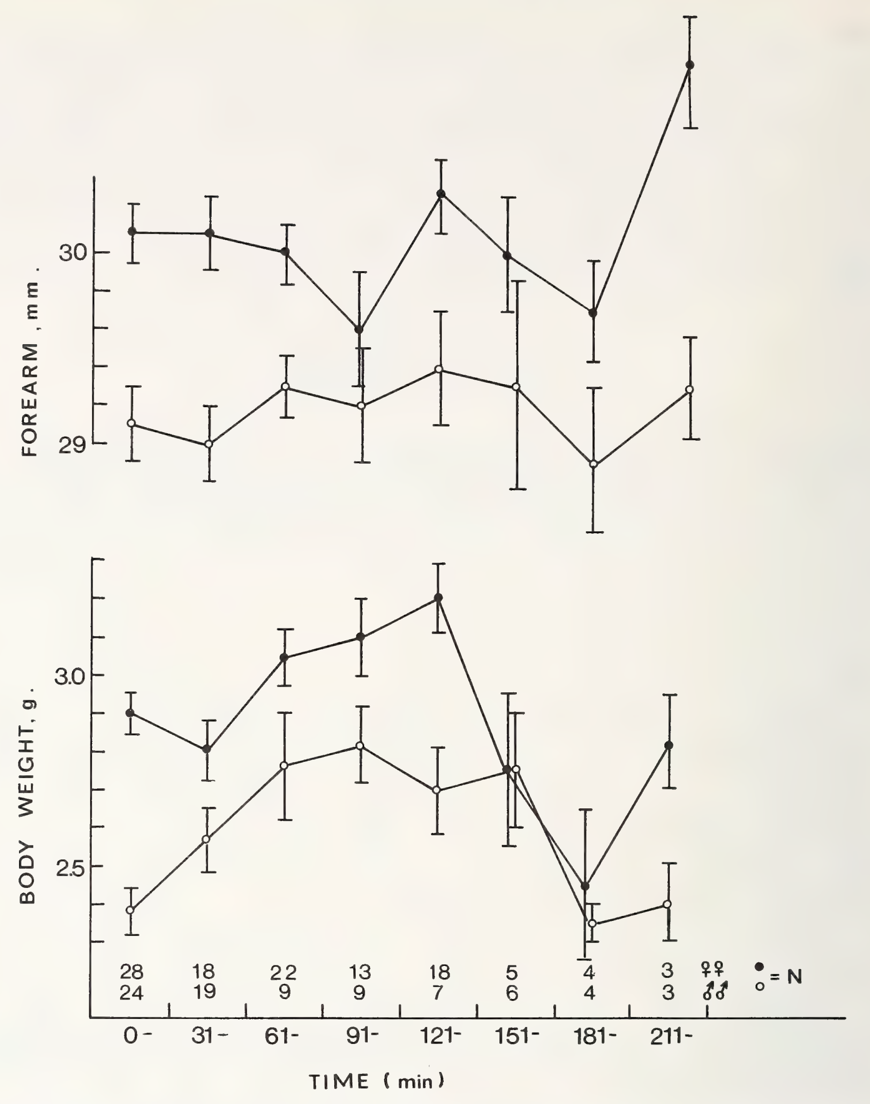


Fig. 3. Mean ± SE body weight and forearm length of male and female *Pipistrellus bodenheimeri* caught in mist nets during the first hours after sunset

had either milk in their milkglands or protruding nipples. There was no evidence of synchronized breeding.

Lactating females were observed from early May until early September and this may indicate that some females give birth twice annually.

Mean body weight fluctuated during the evenings rising from a minimum just after dark to a maximum about 2 hours later and decreased again (Fig. 3). The difference between maximum and minimum body weight was significant for females ($t = 3.14$, $p < 0.001$), but not so in the males ($t = 1.82$, $p = 0.1 > p > 0.05$). Since mean forearm length was similar during this period, it is possible that the increase in body weight was due to intensive feeding by the bats, which added about 15 % to their weight during the first two hours of hunting.

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Zusammenfassung

Die Biologie von Pipistrellus bodenheimeri (Microchiroptera) im Gebiet des Toten Meeres in Israel

Daten über die Biologie von *Pipistrellus bodenheimeri* wurden während einer Untersuchung über die Fledermäuse im Gebiet des Toten Meeres gesammelt. Diese Art kommt während des ganzen Jahres hier vor und überwintert von Oktober bis April. Im Winter wurden nur 5 % der Anzahl von Fledermäusen gefangen, die im Sommer gefangen wurden. Säugende Weibchen wurden von Anfang Mai bis Anfang September gefunden. Weibchen sind deutlich größer und schwerer als Männchen. Diese Fledermäuse fressen am meisten mit Beginn der Aktivitätsphase am Abend und nehmen innerhalb von zwei Stunden 15 % an Gewicht zu.

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Social relations in groups of Black-capped capuchin monkeys, (*Cebus apella*) in captivity: mother-juvenile relations from the second to the fifth year of life

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Abstract

For juvenile black-capped capuchin monkeys the mother is the most attractive social partner in the social group. They approach their mother more frequently than any other group member, prefer to sit in close bodily contact with her and both groom and are groomed by her more frequently than any other group member. With respect to grooming-relations sex-differences become apparent with age. In contrast the mother is of no noticeable importance as a partner in social play.

Introduction

Long-term studies on some primate species living in large social groups reveal that the mother is the most important social partner for her juvenile offspring, continuing even after they reach adulthood. These results are limited to few species of Old World monkeys where long-term studies on individually known animals have been conducted – *Presbytis, Macaca, Papio* – and where many informations are available on Old World monkeys and Great Apes regarding maternal-juvenile interactions (for a review Welker 1985). There are no comparable studies of New World monkeys. In previous reports, on our long-term study of the black-capped capuchin, we reported that the mother is the most attractive animal for the infant (Welker et al. 1987; Welker et al. 1990). This, of course, is true for most mammals and, particularly for primates, the close and prolonged mother-infant bond satisfies both the nutritional and protective needs of a relatively helpless infant. However, to what extent this bond is maintained, after the infant matures and becomes independent, is not known.

Breeding success and a high survival rate in the primate station of Kassel University have yielded quantitative data on mother-juvenile relations in a large sample of black-capped capuchin monkeys, *Cebus apella,* providing us, for the first time, with information on long-term mother-infant relations in a South American primate species living in large social groups. Although these results, obtained under artificial laboratory conditions, do not allow us to extrapolate directly to the wild, we have no reason to believe that the same individual preferences will not be found under natural conditions.

Materials and methods

All 21 *Cebus apella* juveniles, which constituted our sample (see Table), were born into a single social group, the Don group, named after the group's dominant male, at the primate station of Kassel University. The patterns of social behaviour, which occurred regularly and which were scored by trained observers in terms of frequency of occurrence, were: active approach (approaching another individual), passive approach (being approached by another individual), contact sitting, active

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List of capuchin monkeys the authors report on in this paper, observed by group observations (G) of focal-animal samplings (F)

The years of life where data were used are marked (X)

No	Name	Type of observ.	Sex	Date of	Mother	Year of life 2.	3.	4.	5.
25	Pan	G	f	08. 02. 1978	Sylvia			X	X
26	Claudia	F	f	17. 04. 1978	Erna			X	X
27	Daniel	F	m	18. 09. 1978	Dunka			X	X
29	Sarah	G	f	25. 05. 1979	Sylvia		X	X	X
30	Isabelle	F	f	20. 06. 1979	Teufel		X	X	X
31	Christian	F	m	12. 07. 1979	Page		X	X	X
32	Agnes	G	f	17. 07. 1979	Sanga		X	X	X
35	Jonaine	G	f	18. 08. 1980	Teufel	X	X	X	
36	Petra	F	f	19. 09. 1980	Sylvia	X	X	X	X
37	Dennis	F	m	28. 09. 1980	Dunka	X	X	X	X
38	Carlos	G	m	17. 11. 1980	Erna	X	X	X	
40	Lisa[1]	F	f	28. 07. 1981	Sanga	X	X		
41	Justus	F	m	25. 09. 1981	Teufel	X	X	X	X
42	Samuel	F	m	28. 05. 1982	Sylvia	X	X	X	
45	Cesar	F	m	02. 08. 1982	Erna	X	X	X	
46	David	F	m	03. 08. 1982	Dunka	X	X	X	
48	Thomas[2]	F	m	25. 07. 1983	Kim	X			
49	Philipp	F	m	24. 09. 1983	Sylvia	X	X		
53	Jesca	G	f	12. 06. 1984	Teufel	X			
55	Stephanie	G	f	22. 07. 1984	Sarah	X			
56	Karin	G	f	10. 09. 1984	Kim	X			

[1] Lisa died 24. 05. 1984, the data on the third year of life are based on ten months of life, only. – [2] Thomas was separated 27. 06. 1985, the data on the second year of life are based on eleven months of life, only.

grooming, passive grooming, social play. The data were collected by focal-animal observations (F) or group observations (G). As in a previous paper (WELKER et al. 1987) both data sets were combined since both methods revealed no differences between the different age/sex groups when frequency scores were converted to percentages. In the figures the mean of the absolute frequency of the different behaviour patterns protocolled within one year is added (mainly, to give sample sizes for the data sets).

Three of the capuchin juveniles were observed from year 2 to year 5, i.e., for a total of 4 years. The others were observed for from one to three years. The total number of juvenile years covered was 53, 36 of which were by the focal-animal-sampling method and 17 of which were by the group-observation method.

The focal-animal sampling method (in sensu ALTMANN 1974) was used on 13 animals while "all occurrences of some behaviors" were scored for the remaining 8 animals. The focal-animal sampling method provides a complete record not only of the focal animal's actions, but also of behaviours directed to it by others. Each focal animal was observed daily for 15 minutes each minute being a separate entity such that if one behaviour pattern lasted 10 minutes it was scored 10 times. Group observations were conducted daily for 60 minutes each two minutes being regarded as a separate unit such that if one behaviour pattern lasted for 10 minutes it was scored 5 times. All observation sessions were conducted randomly during the period from 3.00 p.m. to 7.00 p.m., according to an established schedule.

The frequency with which juveniles made contact with the mother, in terms of the various categories of behaviour scored, converted to a percentage, was compared statistically with an expected percentage based on the assumption that all members of the group are equally attractive as social partners. Subject to minor fluctuations in group size, over the period of time during which this research was conducted, this value would be about the same for all mother-juvenile dyads observed.

All statistical tests were performed using the Mann-Whitney test with the level of statistical significance set at $p < 0.05$. The data of one individual collected over one year was taken as one independent sample for statistical purposes.

Results

Figure 1 indicates that both male juveniles (Year 2, $p < 0.001$; Year 3, $p < 0.001$; Year 4, $p < 0.005$; Year 5, $p < 0.05$) and female juveniles (Year 2, $p < 0.005$; Year 3, $p < 0.025$; Year 4, $p < 0.001$; Year 5, $p < 0.005$) approach their mothers significantly more often than expected, females significantly more often than males of the same age (Year 3, $p < 0.025$ and Year 4, < 0.005 respectively). Even at five years the same trend is still apparent ($p < 0.1$). These differences hold whether we compare absolute or percentage frequencies from the third year of life on. The higher percentage frequency of approaches to the mother by juvenile daughters in the second year of life is due to the fact that they approach group members less frequently than do males.

Figure 2 reveals that sons and daughters were approached by their mothers significantly more often than expected (sons – Year 2, $p < 0.001$; Year 3, $p < 0.001$; Year 4, $p < 0.005$; Year 5, $p < 0.05$: daughters – Year 2, $p < 0.005$; Year 3, < 0.025; Year 4, $p < 0.005$; Year 5, $p < 0.005$). From four years daughters were approached by their mothers significantly more frequently than were sons ($p < 0.05$). This difference between the sexes is not upheld statistically, however, if absolute frequencies are compared instead of percentage frequencies. With the exception of the fifth year of life, when males were approached less often than were females by their mothers, there was no difference between the sexes in this regard.

The behaviour pattern most frequently observed among mothers and juvenile offspring is contact sitting. Figure 3 shows that, for all four age categories under consideration, mothers sit in close contact with both sons and daughters significantly more frequently than with other group members (sons – Year 2, $p < 0.001$; Year 3, $p < 0.001$; Year 4, $p < 0.005$; Year 5, $p < 0.025$: daughters – Year 2, $p < 0.001$; Year 3, $p < 0.005$; Year 4, $p < 0.001$; Year 5, $p < 0.005$).

Grooming is a particularly important social behaviour and figure 4 reveals that both daughters and sons, irrespective of age, groom their mothers significantly more frequently than they groom other group members (sons – Year 2, $p < 0.025$; Year 3, $p < 0.05$; Year 4, $p < 0.005$; Year 5, $p < 0.05$: daughters – Year 2, $p < 0.001$; Year 3, $p < 0.005$; Year 4, $p < 0.001$; Year 5, $p < 0.005$). At each age level, and in terms of both absolute frequency and percentage frequency, daughters groom their mothers more frequently than do sons these differences being significant from year 3 (Year 3, $p < 0.025$; Year 4, $p < 0.005$; Year 5, $p < 0.05$). The tendency to groom the mother increases with age.

Figure 5 shows that mothers groom both their male and female juvenile offspring significantly more frequently then they groom other members of the social group (sons – Year 2, $p < 0.001$; Year 3, $p < 0.001$; Year 4, $p < 0.005$; Year 5, $p < 0.05$: daughters – Year 2, $p < 0.001$; Year 3, $p < 0.005$; Year 4, $p < 0.001$; Year 5, $p < 0.005$). Male juveniles are relatively more attractive to their mothers than are female juvenile offspring. Interest on the part of the mother in grooming her infants of either sex declines with age.

When one considers both active and passive grooming together (Figs. 4 and 5, absolute frequencies) it is clear that, as they become older, daughters become the more active partners in the mother-infant dyad.

In contrast to the affiliative behaviour patterns mentioned thus far, figure 6 reveals that the mother is of no more importance as a partner in social play to her juvenile offspring of either sex than are other group members and, in fact, is of significantly less importance as a partner in social place to her juvenile sons than are other members of the social group (Year 2, $p < 0.001$; Year 3, $p < 0.001$; Year 4, $p < 0.005$; Year 5, $p < 0.025$).

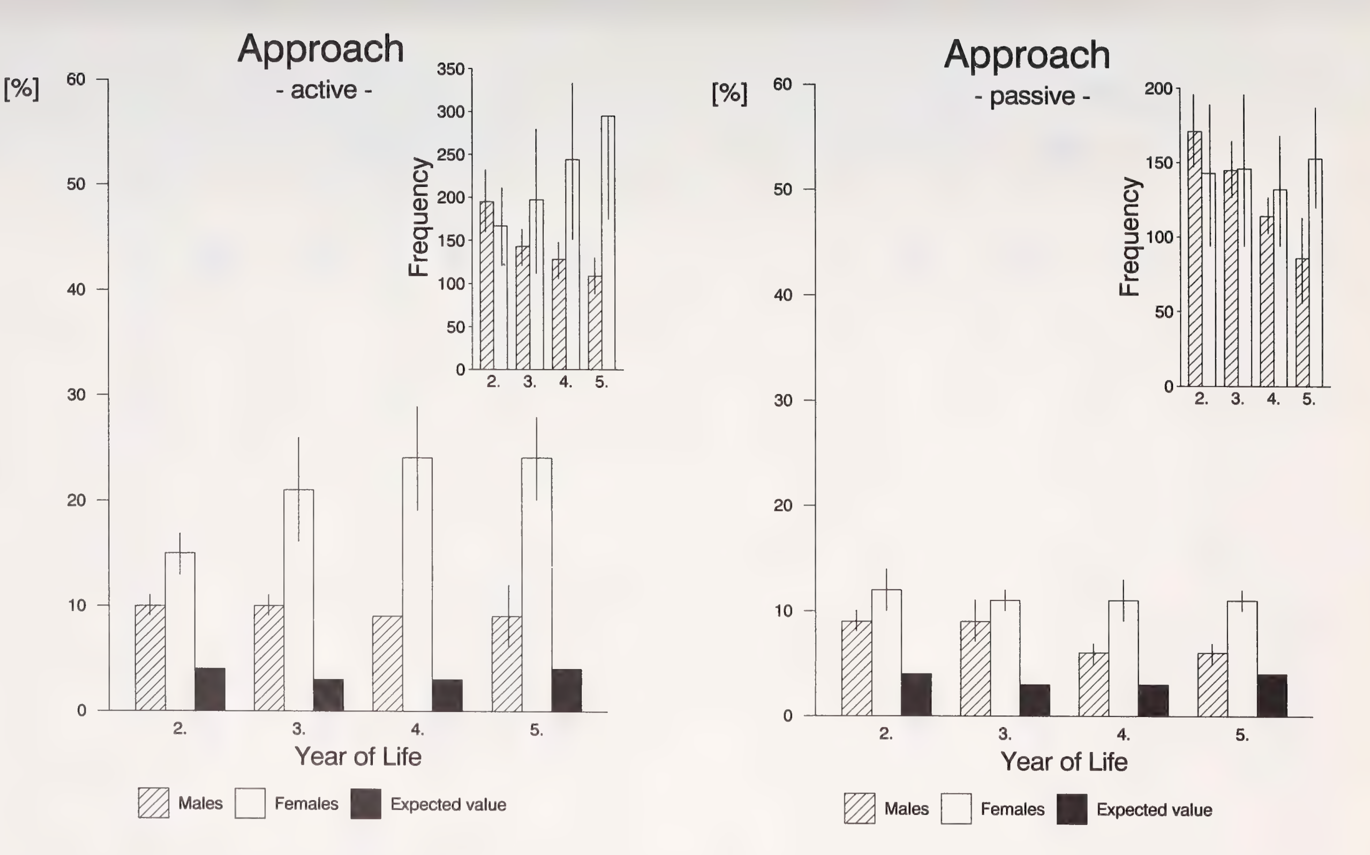


Fig. 1 (left). Active approach – Mean percentage of the frequency of occurrence, together with the standard error of the mean of male and female offspring towards their mother from year 2 to year 5, compared to an expected mean frequency based on the assumption that all members of the group are equally preferable as social partners. In addition the mean absolute frequency (with standard error) is given above on the right hand side. – *Fig. 2 (right).* Passive approach. (As for figure 1)

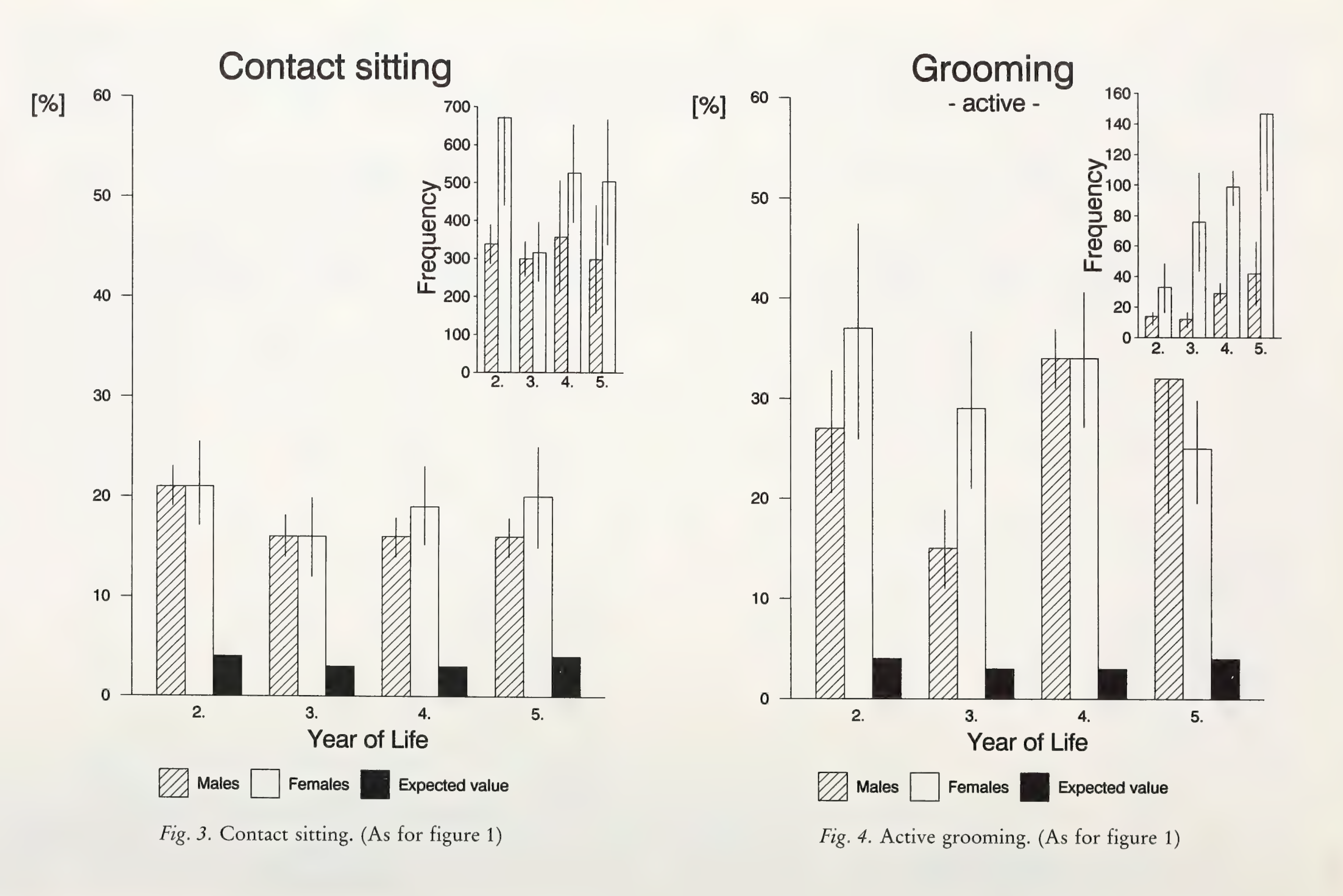


Fig. 3. Contact sitting. (As for figure 1)

Fig. 4. Active grooming. (As for figure 1)

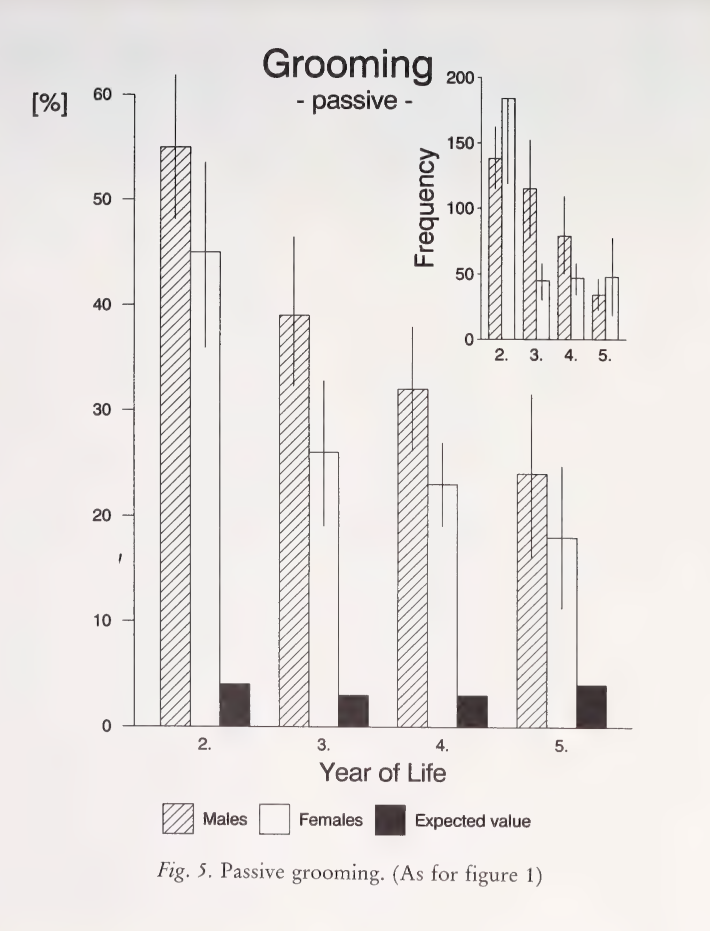


Fig. 5. Passive grooming. (As for figure 1)

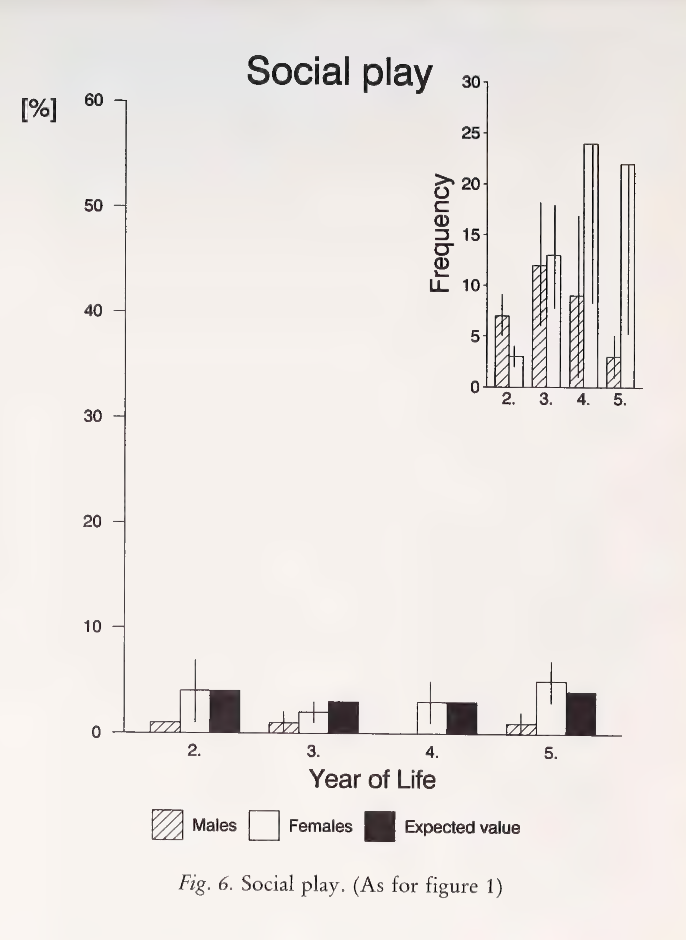


Fig. 6. Social play. (As for figure 1)

Discussion

In juvenile black-capped capuchins the mother remains the most important individual in the social group irrespective of the age of the juvenile. Contact established in the first year of life of the infant (Welker et al. 1987, 1990) is important for the juvenile growing up within the social group, irrespective of the presence of younger siblings. With regard to the behaviour patterns contact sitting, approach and grooming, relations between mothers and juvenile offspring are especially close. These data may be compared with those from other primate species. The results suggest that in South American primates generally, and certainly in the black-capped capuchin, kin-relations are important for the development of the individual living in a social group. The data in respect of contact sitting suggest a particularly close relationship between mothers and daughters. While the reciprocal grooming relationship between mothers and offspring remains close throughout the juvenile period it is with respect of this category of social behaviour that differences between sons and daughters begin to emerge. In the mother-son dyad the mother remains the more active partner while, in the mother-daughter dyad, the daughter becomes the more active partner approaching her mother more frequently and grooming her more frequently than the mother approaches and grooms her daughter. In this way daughters appear both to establish and maintain close relations with their mothers thereby forming matri-clans and kin-based subgroups within the social group. Contact between mothers and sons, on the other hand, declines with age. This gradual weakening of kin relationships suggests a paving of the way, under natural conditions, for the male eventually to leave the social group into which he was born.

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Zusammenfassung

Soziale Beziehungen in Gruppen des Gehaubten Kapuzineraffen (Cebus apella) in Gefangenschaft: Beziehungen zwischen Mutter und Jungtier vom zweiten bis zum fünften Lebensjahr

Für Jungtiere des Gehaubten Kapuzineraffen ist die Mutter der wichtigste Sozialpartner der Gruppe. Sie suchen ihre Mutter häufiger auf als irgendein anderes Gruppenmitglied, sitzen mit ihr in engem Körperkontakt, putzen sie häufiger als andere Kapuzineraffen und werden von ihr gleichfalls auffällig häufig geputzt. Als Spielpartner ist die Mutter jedoch für ihre heranwachsenden Kinder durchgängig unattraktiv. Geschlechtstypische Unterschiede im Verhalten sind vor allem bei der gegenseitigen sozialen Körperpflege aufzeigbar. Mit zunehmendem Alter werden hier Töchter die aktiveren Partner in der Mutter-Kind-Dyade, Söhne dagegen bleiben die passiveren.

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A morphometric analysis of cranial variation in Holarctic weasels (*Mustela nivalis*)

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Abstract

Morphometric relationships of Holarctic weasels (*Mustela nivalis*), based on cranial variables, were analyzed by multiple discriminant function analysis. The results show that all geographic populations of this weasel, except the Egyptian weasel (*subpalmata*), form part of a morphological continuum, thus supporting the contention that they represent one species. The greatest amount of variation is found in the western Palearctic, which suggests that the species has a long history in that part of the world and probably evolved there. The morphometric groupings do not correspond to current infraspecific classification in detail. A division of *M. nivalis* into three subspecific groups is supported by the data. These are: 1. *nivalis*, comprising all small forms of the boreal zones of the Holarctic Region; 2. *vulgaris*, the intermediate to large forms inhabiting the temperate and mediterranean areas of the western Palearctic and 3. *pallida*, a central Asian form. The evidence suggests that the Egyptian weasel is a separate species, *M. subpalmata*.

Introduction

The least weasel (*Mustela nivalis*) has an extensive Holarctic distribution stretching from North Africa and Europe across Asia into North America. Over this vast area this mustelid displays such an unparalleled degree of variation, particularly in size, that the systematic relationships among different geographic populations have long been uncertain.

More than five decades ago, G. M. Allen (1933) combined the small forms from North America and northern Asia into one species. In this regard he followed Kuroda (1921), who had previously described a new Japanese form as a subspecies of the North American least weasel (*M. rixosa*). Shortly after, Ognev (1935) recognized a single species of small weasel, *M. nivalis*, in the Palearctic Region, a view shared by Ellerman and Morrison-Scott (1951). The latter authors stated that the same species perhaps also occurred in North America. On that continent most mammalogists, following Hall (1951) and Hall and Kelson (1959), continued to regard the North American least weasel as a distinct species, *M. rixosa*. Later, Hall (1981) changed his opinion and included the American form in *M. nivalis*, citing Reichstein (1957) for the change. However, Reichstein's study focused on geographic variation and sexual dimorphism in Europe. The analysis of his data led him to the conclusion that the small morph ("Zwergwiesel", *M. minuta* Pomel) is not specifically distinct from the larger morph ("Mauswiesel", *M. nivalis* L.). However, the conclusion that North American and Eurasian small morph weasels are conspecific was not based on his own analysis, but Reichstein (1957) attributes it to a personal communication from Zimmermann. Subsequent studies on large numbers of skins and skulls from Europe (Mazak 1970), on chromosomes (Mandahl and Fredga 1980) and experimental cross-breeding (Frank 1985) all support the earlier conclusion that there is only one species *M. nivalis* in Eurasia and that the small form is only subspecifically distinct. Cytogenetic comparisons of Eurasian and North American weasels (Jarrell 1983) extend this support to the inclusion of the Nearctic least weasel, *M. rixosa*, in *M. nivalis*. Despite

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the evidence in support of a single species, the belief that two species coexist in some areas continued to persist and some authors (KURTÉN and ANDERSON 1980; CORBET 1987) maintained that the taxonomic uncertainty had not been adequately resolved. The lack of direct morphometric comparisons among populations from the entire distributional range has, undoubtedly, contributed to the persistence of this uncertainty. The present study aims at filling this lacuna, by taking a global view of the morphometric interrelationships among populations across the entire Holarctic range.

The objectives of the present study are to: 1. analyze and describe cranial variability in *M. nivalis* across its entire distributional range, using a multivariate approach; and 2. reevaluate the taxonomic status and evolutionary relationships of small and large morphs.

Materials and methods

The total sample on which this study is based, comprised 542 adult skulls, including 263 skulls examined and measured by me, supplemented by data on 279 skulls published by REICHSTEIN (1957). The breakdown by subspecies, sex, locality and collection of the specimens examined, arranged by nominal subspecies and geographic subsamples, is as follows: BM = British Museum of Natural History; USNM = U. S. National Museum of Natural History; NMC = Canadian Museum of Nature; APM = Alberta Provincial Museum.

M. n. nivalis: 12 males, 2 females, 3 undetermined. Northern Europe: males, Norway 1 (BM); Sweden 1 (USNM); females, Russia 1 (BM); Western Siberia: males, 10 (NMC); females 1 (BM); undetermined 3 (BM).

M. n. vulgaris: 47 males, 15 females, 3 undetermined. Western Europe: British Isles, males 9 (BM), 5 (USNM), females 5 (USNM), undetermined 2 (USNM); France, males 6 (BM), 4 (USNM), females 1 (BM), undetermined 1 (BM), Netherlands, males 12 (BM), females 2 (BM), 1 (USNM); Central Europe: Czechoslovakia, males 1 (USNM), females 1 (BM), Hungary, males 1 (BM), Germany, males 3 (BM), females 1 (USNM), Roumania, males 1 (USNM), Switzerland, males 5 (USNM), females 4 (USNM).

M. n. boccamela: 30 males, 10 females, 3 undetermined. Italy and Mediterranean France: France, males 1 (BM); Italy, males 3 (BM), 4 (USNM), females 1 (BM), undetermined 1 (BM), Sardinia, males 2 (BM), Sicily, males 2 (BM), Balkan Peninsula: Greece, males 1 (BM), Crete, males 1 (BM), Yugoslavia, males 3 (BM), females 1 (BM), Iberian Peninsula: Spain, males 5 (BM), 1 (USNM), females 2 (BM), 2 USNM), undetermined 1 (BM), Azores, undetermined 1 (BM), Balearic Islands, males 1 (BM), females 1 (BM); Southwestern Asia: Afghanistan, males 1 (BM), Turkey, males 4 (BM), 1 (USNM), females 1 (BM), 1 (USNM), Iran, males 1 (BM), females 1 (BM).

M. n. numidica: 3 males, 1 undetermined. Northwest Africa: Algeria, males 2 (BM), Morocco, males 1 (USNM), Tunis, undetermined 1 (BM).

M. n. subpalmata: 8 males, 9 females, 2 undetermined. Egypt: males 3 (BM), 5 (USNM), females 3 (BM), 6 (USNM), undetermined 2 (USNM).

M. n. pallida: 6 males, 1 undetermined. Central Asia: Djarkent (= Panfilov), males 6 (BM), undetermined 1 (BM).

M. n. pygmeae: 24 males, 5 females, 1 undetermined. Eastern Siberia: males 21 (USNM), females 4 (USNM), Eastern Asia: Korea, males 1 (USNM), females 1 (USNM), Manchuria, males 2 (USNM), undetermined 1 (USNM).

M. n. russelliana: Szechwan, females 1 (BM).

M. n. rixosa: 26 males, 15 females, 2 undetermined. Canada: Alberta, males 2 (NMC), 6 (APM), females, 2 (NMC), 5 (APM), undetermined 1 (APM), British Columbia, males 5 (NMC), Manitoba, males 1 (NMC), Northwest Territories, males 3 (USNM), 4 (NMC), females 2 (NMC), undetermined 1 (NMC), Quebec, males 1 (NMC), Saskatchewan, males 4 (NMC), females 6 (NMC).

M. n. allegheniensis: 11 males, 4 females. Eastern United States: Indiana, males 5 (USNM), females 1 (USNM), Maryland, females 1 (USNM), North Carolina, males 1 (USNM), Pennsylvania, males 1 (USNM), females 1 (USNM), Tennessee, males 1 (USNM), Virginia, males 1 (USNM), West Virginia, males 2 (USNM), females 1 (USNM).

M. n. campestris: 7 males, 3 females; Central Great Plains: Missouri, males 2 (USNM), females 2 (USNM), North Dakota, males 3 (USNM), South Dakota, males 2 (USNM), females 1 (USNM).

M. n. eskimo: 4 males, 4 females, undetermined 2; Alaska-Yukon: Alaska, males 1 (USNM), 1 (NMC), females 3 (USNM), undetermined 1 (NMC), Yukon, males 2 (NMC), females 1 (NMC), undetermined 1 (NMC).

There is no generally accepted subspecific classification of *M. nivalis*. In the main, I have followed Ellerman and Morrison-Scott (1951) in the application of subspecific names to Palearctic populations, with some modifications based on Heptner et al. (1974). For North American forms I have followed Hall (1981). Specimens of undetermined sex were diagnosed by discriminant function analysis and included in the appropriate sample.

Thirteen measurements were made on each skull, using a digital caliper capable of measuring to 0.01 mm. The cranial measurements taken (as defined by van Zyll de Jong 1972, except for #1), are: 1, condylobasal length (CBL); 2, interorbital width (IOW); 3, width between postorbital processes (WPOP); 4, orbitonasal length (ONL); 5, width of the postorbital constriction (WPOC); 6, basal skull width (BSW); 7, mastoid width (MW); 8, zygomatic width (ZW); 9, buccal length of P4 (LP4); 10, greatest width of P4 (GWP4); 11, lingual length of M1 (LM1); 12, greatest diameter of M1 (GDM1); 13, length of the mandibular premolar-molar series (Lpm). Measurements 1, 2, 7 and 8 were supplemented with data from Reichstein (1957).

Multigroup discriminant function analysis (BIOSTAT II MDA, Pimentel and Smith (1986) was used to discriminate among geographic samples of weasels using 12 variables. This analysis was done to assess the global variation in size and shape of the skull. The geographic areas and nominal subspecies represented in the analysis comprised the following: 1. Canada (*rixosa*); 2. eastern United States (*allegheniensis*); 3. central Great Plains (U. S.) (*campestris*); 4. Alaska-Yukon (*eskimo*); 5. eastern Siberia (*pygmaea*); 6. eastern Asia (*pygmaea*); 7. central Asia (*pallida*); 8. western Siberia (*nivalis*); 9. northern Europe (*nivalis*); 10. central Europe (*vulgaris*); 11. western Europe (*vulgaris*); 12. southwestern Asia (*boccamela*); 13. Balkan Peninsula (*boccamela*); 14. Italy and adjacent mediterranean France (*boccamela*); 15. Iberian Peninsula (*iberica*); 16. northwest Africa (*numidica*); 17. Egypt (*subpalmata*).

A smaller number of variables, but a larger number of geographic samples (including Reichstein's data) were used to increase resolution in the area of greatest geographic variation. The geographic areas represented in this analysis were as above, but central Europe is represented by separate samples for: 1. northern Germany; 2. central and western Germany; 3. southern Germany; 4. Silesia; 5. Poland; 6. Switzerland; and 7. Sardinia is separated from Italy.

Both sets of samples were also subjected to distance analysis, using the generalized distance (D), to study the morphometric relationships among geographic poulations. To this end, the matrix of generalized distances among geographic forms was analyzed by cluster analysis (UPGMA, Sneath and Sokal 1973). Males and females were analyzed separately.

Results

Cranial variation in males

The results of the multiple discriminant function analysis of the subsamples of males are presented in table 1 and figure 1. The graph (Fig. 1) shows the centroid of each group and the dispersion of individuals around them (polygons) plotted onto the first two canonical variates. The relative importance of the different variates in the discrimination of samples is listed in table 1 and shown by the character vector diagram in figure 1. A little over 70 percent of the cranial variation is explained by the first canonical axis, 16.29 percent by the second and 4.11 by the third axis (Table 1). All variates, except ONL contribute to a considerable extent to discrimination on the first axis. This axis discriminates among size classes, from small on the left to large on the right. On the second axis, BSW and GWP4 contribute to discrimination to an important degree (Table 1).

The bivariate plot of the centroids and their respective polygons clearly shows an ordination into two separate nonoverlapping groups, with *M. n. subpalmata* on the one hand and all the other geographic samples on the other. A closer examination reveals that the latter group is composed of two, or three, subsidiary groupings. On the left of the graph we see the largely overlapping polygons representing the small North American, Siberian, eastern Asian and northern European forms and on the right a similar overlapping cluster of the larger forms from temperate Europe, the Mediterranean area and southwestern Asia. These two clusters are linked by the sample from central Europe. A

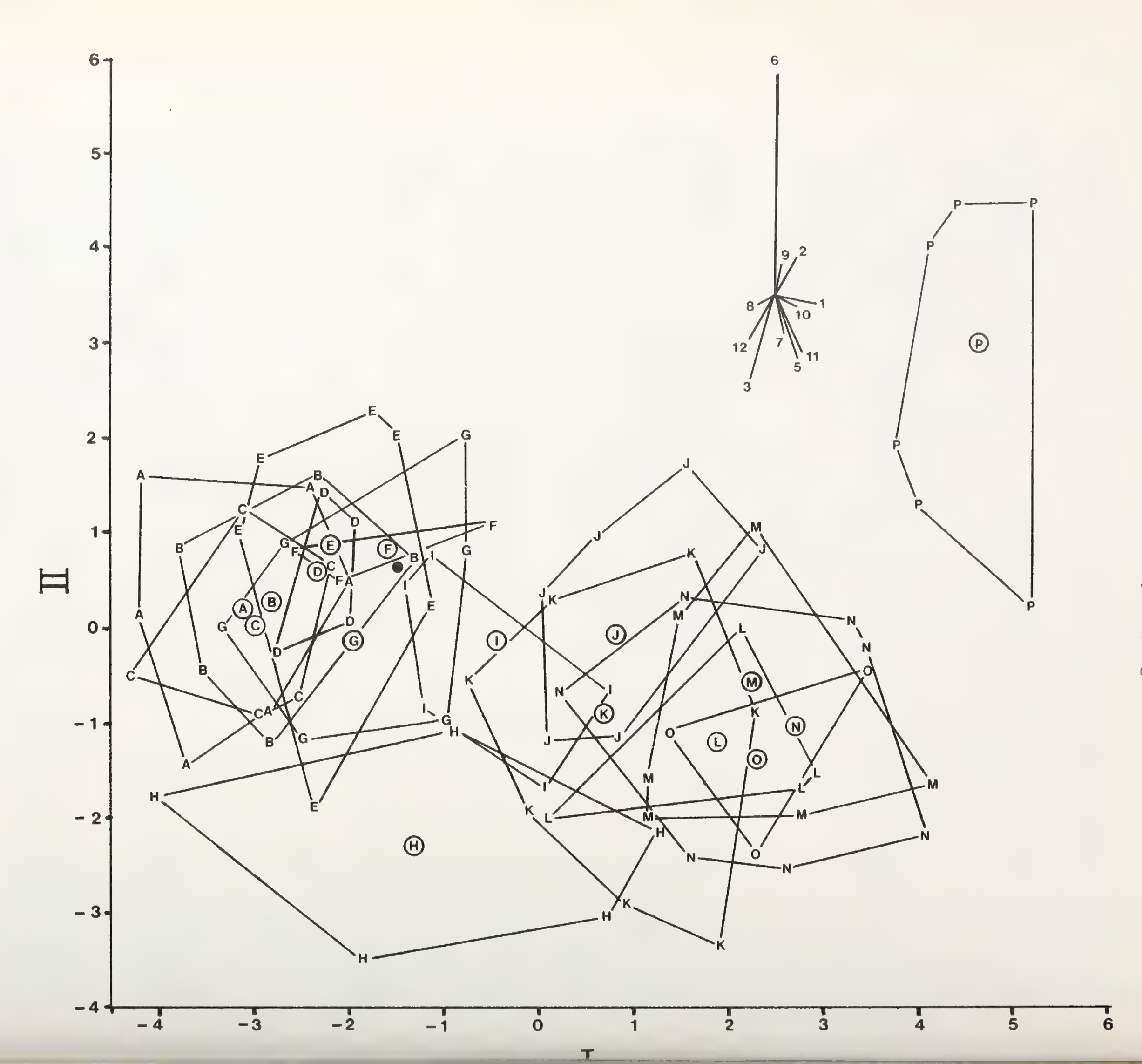


Fig. 1. Graph showing the projection of the centroids and sample dispersions (polygons) of 16 geographic samples of *Mustela nivalis* males onto the first two canonical axes. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*allegheniensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Eastern Asia (*pygmaea*); G: Western Siberia (*nivalis*); H: Central Asia (*pallida*); I: Central Europe (*vulgaris*); J: Iberian Peninsula (*iberica*); K: Western Europa (*vulgaris*); L: Southwestern Asia (*boccamela*); M: Italy and adjacent areas (*boccamela*); N: Balkan Peninsula (*boccamela*); O: Northwestern Africa (*numidica*); P: Egypt (*subpalmata*). The solid dot represents the centroid of two specimens from northern Europe (*nivalis*). The character vector diagram illustrates the relative contribution of the original variables to the canonical variates (numbers as listed in the text)

Table 1. **First three standardized canonical vectors from the discriminant function analysis of 12 cranial variables from *Mustela nivalis***

The number in parentheses is the percentage of the variance of each variable contributed to the canonical axis

Variable	Standardized canonical vectors 1	2	3	Cumulative percent
1. CBL	0.451 (92.53)	−0.070 (0.13)	−0.024 (0.00)	92.66
2. IOW	0.203 (69.73)	0.388 (15.35)	0.602 (2.09)	87.17
3. WPOP	−0.232 (50.16)	−0.881 (43.40)	0.250 (0.20)	93.76
4. ONL	−0.014 (1.22)	−0.048 (0.90)	−0.810 (14.27)	16.39
5. WPC	0.267 (64.66)	−0.635 (22.13)	0.027 (0.00)	86.79
6. BSW	0.026 (0.20)	2.331 (95.28)	−0.748 (0.55)	96.03
7. MW	0.119 (41.55)	−0.395 (27.50)	0.994 (9.84)	78.89
8. LP4	−0.171 (81.84)	−0.088 (1.30)	0.687 (4.48)	87.62
9. GWP4	0.071 (40.69)	0.304 (45.10)	0.005 (0.00)	85.79
10. LM1	0.263 (96.16)	−0.120 (1.21)	−0.267 (0.34)	97.71
11. GDM1	0.310 (69.10)	−0.605 (15.83)	0.894 (1.95)	86.88
12. Lpm	−0.254 (71.83)	−0.458 (14.04)	−1.712 (11.05)	96.92
Percent trace	70.70	16.29	4.11	
Cumulative percent	70.70	86.99	91.09	

Test of equality of group centroids: $F = 7.35$ with 96 and 1081 degrees of freedom. $P < 0.001$.

Table 2. **First two standardized canonical vectors from the discriminant function analysis of four cranial variables from *Mustela nivalis* males**

Numbers in parentheses represent the percentage of the variance of each variable contributed to the canonical vector

Variable	Standardized canonical vectors 1	2	Cumulative percent
1. CBL	−0.698 (98.13)	−1.258 (1.19)	99.32
2. IOW	0.122 (72.86)	−0.484 (4.31)	77.17
3. MW	−0.399 (86.62)	2.544 (13.27)	99.89
4. ZW	−0.036 (11.04)	−0.919 (26.85)	37.89
Percent trace	87.78	6.95	
Cumulative percent	87.78	94.73	

Test of equality of group centroids: $F = 11.46$ with 88 and 1905 degrees of freedom. $P < 0.0001$.

third subsidiary group is represented by the small sample from Central Asia situated below, and marginally overlapping the two previous groups. The character vectors (Fig. 1 and Table 1) indicate that the boreal and temperate weasels differ from one another principally in size, lying along a common size axis, which slopes gently from left to right. The sample from central Asia is somewhat intermediate in size relative to the last to groups, but differs from them to some extent in the shape of the skull (relatively greater WPOP, WPC and Lpm). The Egyptian weasel (*subpalmata*), on the other hand, differs from all the others in size, as well as in shape (relatively broader BSW, GWP4 and IOW).

The results of a UPGMA cluster analysis of the matrix of Generalized Distances among the geographic populations are shown in the form of a phenogram (Fig. 2). All small northern forms make up one cluster, which is joined by the central Asian form at a lower

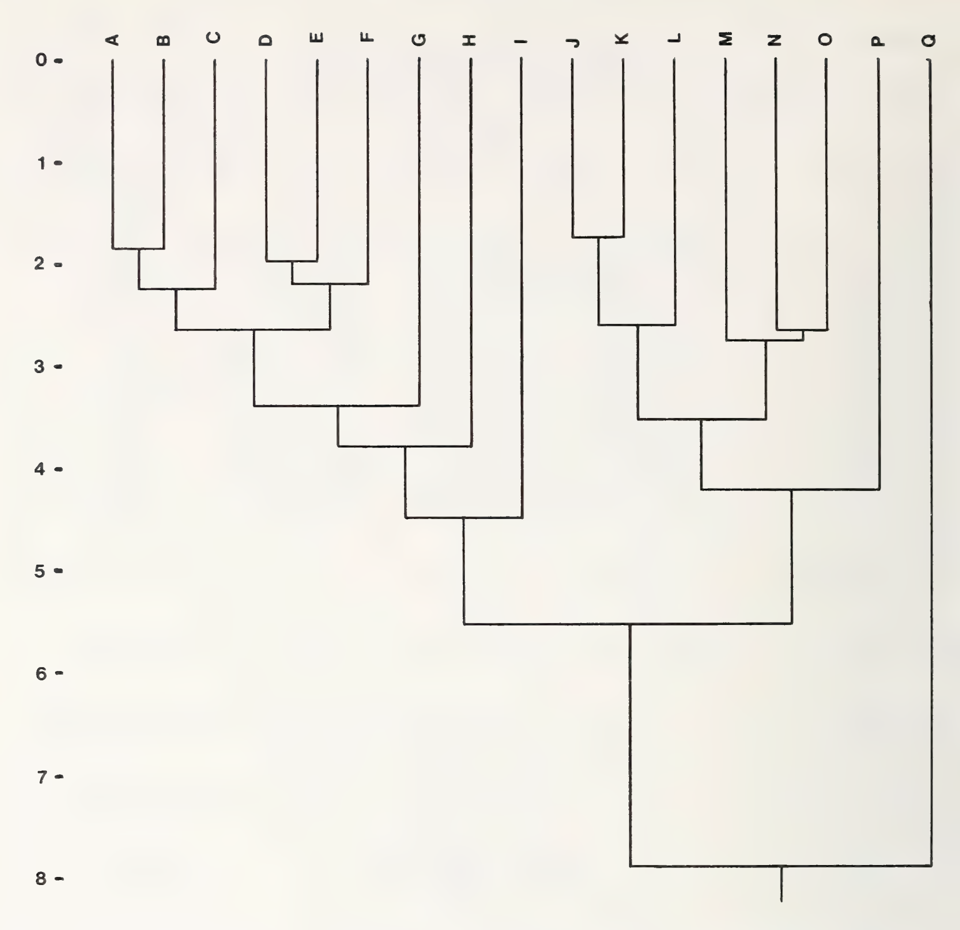


Fig. 2. Distance phenogram summarizing the morphometric relationships among 17 geographic samples of male *Mustela nivalis.* A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Western Siberia (*nivalis*); D: Eastern Siberia (*pygmaea*); E: Eastern Asia (*pygmaea*); F: Northern Europe (*nivalis*); G: Eastern U.S. (*allegheniensis*); H: Central Great Plains, U.S. (*campestris*); I: Central Asia (*pallida*); J: Balkan Peninsula (*boccamela*); K: Italy (*boccamela*); L: Southwestern Asia (*boccamela*); M: Central Europa (*vulgaris*); N: Iberian Peninsula (*iberica*); O: Western Europe (*vulgaris*); P: Northwestern Africa (*numidica*); Q: Egypt (*subpalmata*)

level (4.47), and all large temperate and southern forms constitute a similarly structured cluster. The Egyptian weasel is most remote and joins the others at D = 7.91.

It is clear from examining the above results, that the greatest cranial variation is found in the western Palearctic. Results of the discriminant function analysis of a larger number of geographic samples, but a smaller number of variates (CBL, IOW, MW, and ZW, including REICHSTEIN's [1957] data) provided increased resolution of the general pattern of variation in this area. The broad pattern of geographic variation that emerged from the analysis is depicted in two ways. Firstly, the results are shown as a graph of the centroids and their 95 % confidence circles on the first two canonical axes (Fig. 3). Secondly, to place the variation in a geographical context, the results are projected on a map of the distributional range as graphic indices of each population's morphometric state and as generalized distances between neighboring populations (Fig. 4).

The plot of the centroids shows the weasel populations arranged from small, on the

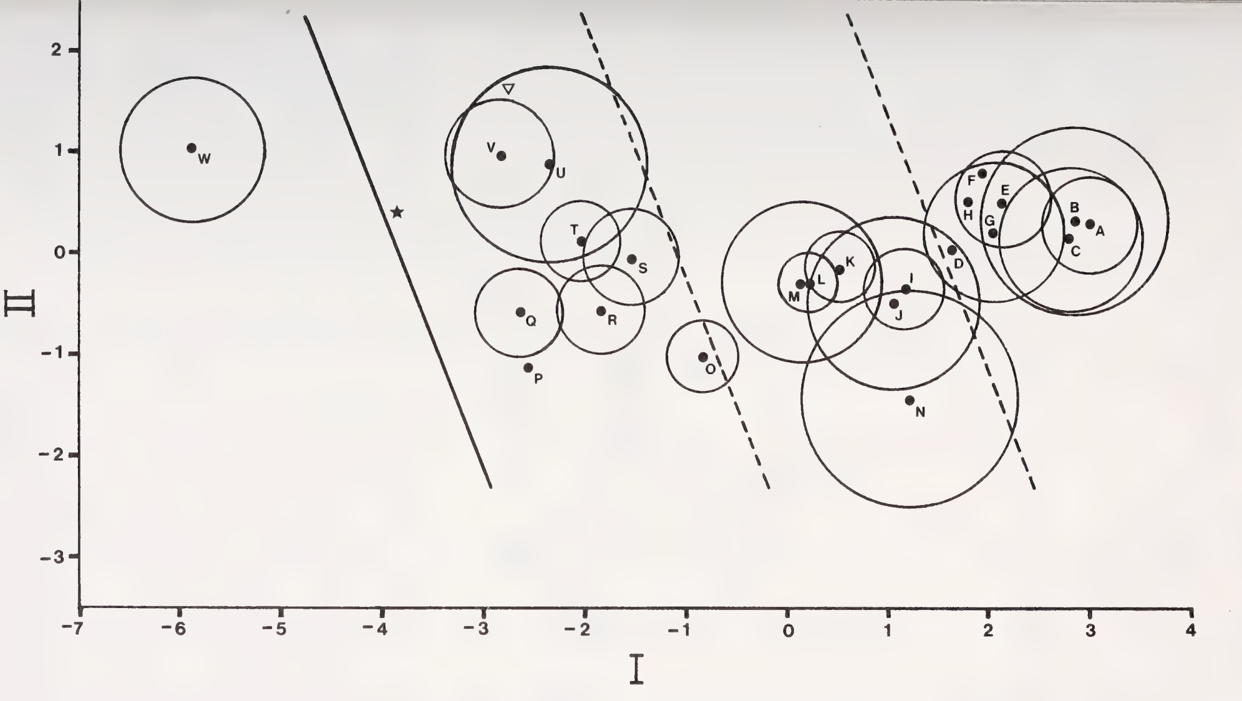


Fig. 3. Canonical graph (axes 1 and 2) of the centroids and their respective 95 % confidence circles of 23 geographic samples of male *Mustela nivalis* based on four cranial variables. The broken diagonal lines separate overlapping forms of *M. nivalis* ranging from small on the right to intermediate and large on the left. The solid diagonal line marks the separation of *subpalmata*, which does not overlap with the other forms. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*allegheniensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Eastern Asia (*pygmaea*); G: Western Siberia (*nivalis*); H: Northern Europa (*nivalis*); I: Switzerland (*vulgaris*); J: Southern Germany (*vulgaris*); K: Western and central Germany (*vulgaris*); L: Northern Germany (*vulgaris*); M: Poland (*vulgaris*); N: Central Asia (*pallida*); O: Western Europe (*vulgaris*); P: Northwestern Africa (*numidica*); Q: Balkan and Danube states (*boccamela*); R: Silesia (*vulgaris*); S: Iberian Peninsula (*iberica*); T: Italy (*boccamela*); U: Southwestern Asia (*boccamela*); V: Sardinia (*boccamela*); W: Egypt (*subpalmata*). Two single specimens from the Azores and Crete (*galianthas*), inverted triangle and star respectively, were scored a posteriori and plotted to show their morphometric relationships

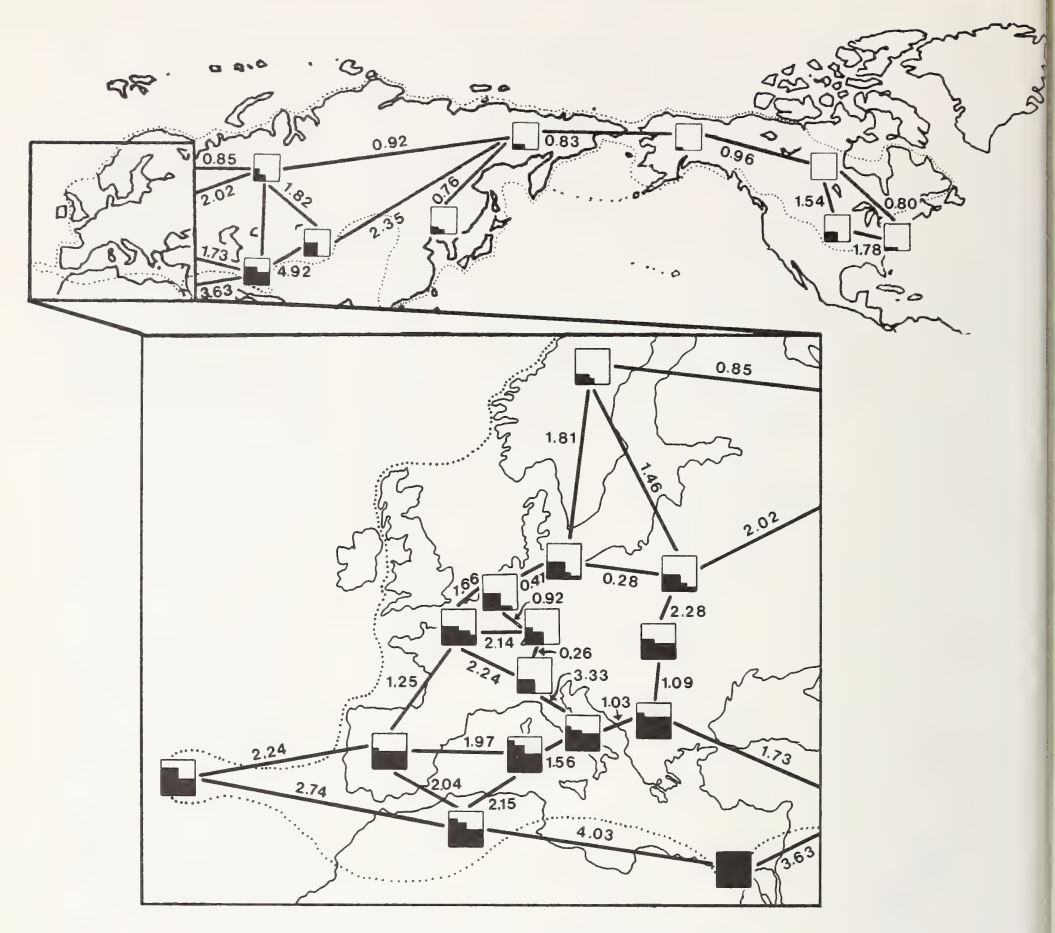


Fig. 4. Geographic variation in the skulls of male *Mustela nivalis*. The squares indicate the morphometric position of the regional forms on the first canonical axis from smallest (no black) to largest (all black). The numbers and lines joining the squares give the generalized distance (D) and a comparative measure of the spatial separation of neighboring populations represented by the samples. In North America and Asia from east to west: Eastern U.S. (*allegheniensis*); Central Great Plains, U.S. (*campestris*); Canada (*rixosa*); Alaska-Yukon (*eskimo*); Eastern Siberia (*pygmaea*); Eastern Asia (*pygmaea*); Central Asia (*pallida*); West Siberia (*nivalis*) (north); Southwestern Asia (*boccamela*) (south). In Europe and North Africa from north to south and east to west: Northern Europa (*nivalis*); Poland (*nivalis*); Northern Germany (*nivalis*); Central and Western Germany (*vulgaris*); Silesia (*vulgaris*); Southern Germany (*vulgaris*); Western Europe (*vulgaris*); Switzerland (*vulgaris*); Balkan Peninsula (*boccamela*); Italy (*boccamela*); Sardinia (*boccamela*); Iberian Peninsula (*iberica*); Azores; Egypt (*subpalmata*); Northwest Africa (*numidica*)

right, to large forms on the left (see table 2 for standardized canonical vectors). The centroids with their largely overlapping confidence regions form a graded series from small boreal forms to intermediate temperate forms, to large mediterranean forms, whereas the Egyptian weasel is separated from all the others by a distinct gap.

The distribution of morphological forms and D values separating neighbours show clearly that the samples from boreal areas across North America and Eurasia, although separated by large distances in space, differ from each other relatively little morphometrically (Fig. 4). In the western Palaearctic, on the other hand, there is considerable

Table 3. **Results of univariate Newmann-Student-Keuls test on four variables of male weasels**
Sample designations as in Fig. 3

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<tr><th></th><th></th><th>CBL</th><th></th><th colspan="6"></th><th></th><th></th><th>IOW</th><th></th><th colspan="6"></th></tr>
<tr><th>Sample</th><th>N</th><th>Subspecies</th><th>Mean</th><th colspan="6">Subset</th><th>Sample</th><th>N</th><th>Subspecies</th><th>Mean</th><th colspan="6">Subset</th></tr>
<tr><td>A</td><td>18</td><td>rixosa</td><td>31.15</td><td>|</td><td></td><td></td><td></td><td></td><td></td><td>A</td><td>18</td><td>rixosa</td><td>6.34</td><td>|</td><td></td><td></td><td></td><td></td><td></td></tr>
<tr><td>C</td><td>10</td><td>allegh</td><td>31.69</td><td>|</td><td></td><td></td><td></td><td></td><td></td><td>B</td><td>7</td><td>eskimo</td><td>6.61</td><td>|</td><td>|</td><td></td><td></td><td></td><td></td></tr>
<tr><td>B</td><td>7</td><td>eskimo</td><td>31.69</td><td>|</td><td></td><td></td><td></td><td></td><td></td><td>C</td><td>10</td><td>allegh</td><td>6.78</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td></tr>
<tr><td>E</td><td>19</td><td>pygmae</td><td>32.93</td><td>|</td><td>|</td><td></td><td></td><td></td><td></td><td>D</td><td>4</td><td>campes</td><td>6.79</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td><td></td></tr>
<tr><td>F</td><td>3</td><td>pygmae</td><td>33.09</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td><td>F</td><td>3</td><td>pygmae</td><td>6.98</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td></tr>
<tr><td>G</td><td>11</td><td>nivali</td><td>33.34</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td><td>E</td><td>19</td><td>pygmae</td><td>7.01</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td></tr>
<tr><td>H</td><td>5</td><td>nivali</td><td>33.63</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td></td><td>H</td><td>5</td><td>nivali</td><td>7.28</td><td>|</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td></tr>
<tr><td>D</td><td>4</td><td>campes</td><td>34.00</td><td>|</td><td>|</td><td>|</td><td>|</td><td></td><td></td><td>G</td><td>11</td><td>nivali</td><td>7.30</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td></td></tr>
<tr><td>I</td><td>27</td><td>vulgar</td><td>35.13</td><td></td><td>|</td><td>|</td><td>|</td><td></td><td></td><td>I</td><td>27</td><td>vulgar</td><td>7.43</td><td></td><td>|</td><td>|</td><td>|</td><td>|</td><td></td></tr>
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<tr><td>M</td><td>9</td><td>vulgar</td><td>37.02</td><td></td><td></td><td>|</td><td>|</td><td></td><td></td><td>L</td><td>53</td><td>vulgar</td><td>7.98</td><td></td><td></td><td></td><td></td><td>|</td><td></td></tr>
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<tr><td>S</td><td>19</td><td>iberic</td><td>40.20</td><td></td><td></td><td></td><td></td><td>|</td><td>|</td><td>R</td><td>23</td><td>vulgar</td><td>8.77</td><td></td><td></td><td></td><td></td><td></td><td>|</td></tr>
<tr><td>R</td><td>23</td><td>vulgar</td><td>41.00</td><td></td><td></td><td></td><td></td><td></td><td>|</td><td>S</td><td>19</td><td>iberic</td><td>8.89</td><td></td><td></td><td></td><td></td><td></td><td>|</td></tr>
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</table>

morphometric change over relatively small distances, generally taking the form of a north-south cline of increasing size. The smallest morphs occur in northern Europe and the largest in the Mediterranean area. The existence of this size cline was demonstrated previously by REICHSTEIN (1957). Exceptions to this general north-south trend are the populations from higher altitudes in Southern Germany and Switzerland. These are markedly smaller, approaching the boreal forms in size.

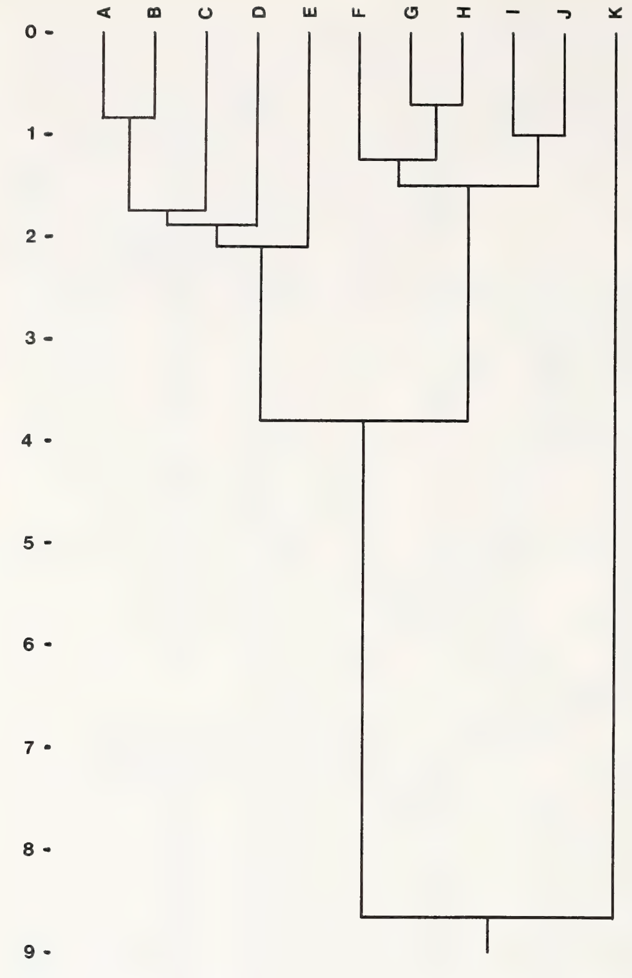


Fig. 5. Distance phenogram summarizing the morphometric relationships of 11 geographic samples of female *Mustela nivalis*. A: Canada (*rixosa*); B: Eastern U.S. (*allegheniensis*); C: Alaska-Yukon (*eskimo*); D: Eastern Siberia (*pygmaea*); E: Central Great Plains, U.S.: (*campestris*); F: Italy (*boccamela*); G: Iberian Peninsula (*iberica*); H: Southwestern Asia (*boccamela*); I: Central Europe (*vulgaris*); J: Western Europe (*vulgaris*); K: Egypt (*subpalmata*)

The results of the a posteriori Student-Newmann-Keuls multiple range test confirm the generally north-south gradual size variation in geographic samples and the gap between *subpalmata* and all the others (Table 3). The only gap, in the largely overlapping nonsignificant subsets, is that between the smaller central European forms (I–L) and the western European-Iberian subset (O–S).

Cranial variation in females

The results of the analyses of female skulls were similar to those obtained for the males. Females were represented in lower numbers in collections and were lacking entirely for some of the geographic subsamples. Because of the reduced geographic representation of females and the similarity of the results for both sexes, it suffices to list the standardized canonical vectors (Table 4) and to show the results of the cluster analysis of the distances among samples of females from different geographic areas (Fig. 5). The clustering of female weasels in three main clusters representing boreal small sized, temperate to mediterranean intermediate-to-large size and Egyptian weasels parallels that of the males closely. The main difference between male and female samples is the generally smaller distance (D) between the female centroids and the larger distance separating the Egyptian females from all the rest.

The results of the analysis of geographic variation based on four characters (Figs 6 and 7), likewise, resemble those of the males closely, with little variation in the north from North America to northern Europe and relatively precipitous size change from north to south in Europe. The smaller intercentroid distances among female samples, compared to those among male samples, are again noticeable, as well as the much greater distance of the *subpalmata* centroid from all others. The results of the Student-Newmann-Keuls test of

Table 4. **First three standardized canonical vectors from a discriminant function analysis of 12 cranial variables from *Mustela nivalis* females**

Numbers in parentheses represent the percentage of the variance of each variable contributed to the canonical vector

Variable	Canonical vectors 1	2	3	Cumulative percent
1. CBL	−0.864 (99.99)	−0.010 (0.00)	−0.026 (0.00)	100
2. IOW	0.514 (82.35)	1.398 (16.44)	1.020 (1.19)	99.98
3. WPOP	0.149 (89.11)	0.019 (0.03)	−0.854 (10.85)	99.99
4. ONL	0.386 (91.98)	−0.634 (6.70)	−0.757 (1.30)	99.98
5. WPC	−0.548 (97.44)	0.499 (2.17)	−0.567 (0.38)	99.99
6. BSW	−0.410 (62.85)	−1.883 (35.75)	1.006 (1.39)	99.99
7. MW	−0.201 (93.10)	0.331 (6.84)	−0.084 (0.06)	100
8. LP4	−0.143 (88.79)	0.310 (11.20)	0.000 (0.00)	99.99
9. GWP4	−0.076 (38.01)	0.491 (43.30)	0.872 (18.68)	99.99
10. LM1	0.344 (98.43)	−0.264 (1.56)	−0.022 (0.00)	99.99
11. GDM1	−0.558 (96.39)	0.657 (3.60)	0.023 (0.00)	99.99
12. Lpm	0.723 (97.76)	−0.592 (1.76)	−0.824 (0.46)	99.98
Percent trace	92.28	6.41	1.30	
Cumulative percent	92.28	98.70	100	

Test of equality of group centroids: F = 7.76 with 36 and 133 degrees of freedom. P < 0.001.

the four variables (Table 5) confirms the continuous nature of the size variation and the smaller differences among female samples, with the obvious exception of the sample of *subpalmata*. The greater difference between *subpalmata* females and females of all the others forms, compared to that in the males, points to the existence of a male-female size relationship in Egyptian weasels that differs from that in the other taxa. This brings us to a consideration of sexual dimorphism of size.

Variation in sexual dimorphism of size

Reichstein (1957) pointed out that the difference in size between the sexes in *M. nivalis* increases with overall size. In the present samples, for instance, the difference in mean condylobasal length of males and females of the small boreal forms is relatively slight, with the length of the female skull averaging 93 % of that of the male skull (range 90–97 %). In the large mediterranean morphs, on the other hand, the difference is much greater. The female skull length in these forms averages only 85 % of the male skull length (range 83–88 %). An apparent exception is the Egyptian weasel. The mean condylobasal length of the female Egyptian weasel sample constituted about 90 % of the mean of the same length in males.

To investigate the relationship of size in females and males further, the logarithm of the mean condylobasal length of females was plotted against that of males of the same geographic population. Inspection of the resulting pattern suggests a linear relationship of size between the sexes in geographic populations of *M. nivalis,* with the exception of the Egyptian sample, which clearly deviates from the common trend (Fig. 8). The equation describing the relationship (Model II regression, Sokal and Rohlf 1981) shows that size in females increases at a lower rate than that in males, i.e. the relation is allometric. The goodness of fit index (r^2 = .86) indicates that the regression describes the relationship effectively. The mean size of the female Egyptian weasel predicted by the regression (38.0 mm) is less than the actually observed value (43.5 mm). Thus the growth rate in females approaches that of the males more closely in this taxon.

Table 5. **Results of univariate Student-Newmann-Keuls test on four variables in female weasels**
Sample designations as in Fig. 6

Sample	N	CBL Subspecies	Mean	Subset	Sample	N	IOW Subspecies	Mean	Subset
A	10	*rixosa*	28.83	│	A	10	*rixosa*	5.78	│
B	5	*eskimo*	29.55	│ │	C	4	*allghe*	6.02	│ │
E	5	*pygmae*	29.59	│ │	E	5	*pygmae*	6.04	│ │
C	4	*allegh*	30.09	│ │	B	5	*eskimo*	6.16	│ │
H	16	*vulgar*	30.82	│ │	D	2	*campes*	6.23	│ │ │
D	2	*campes*	30.96	│ │ │	H	16	*vulgar*	6.27	│ │ │
K	15	*vulgar*	31.14	│ │ │	K	15	*vulgar*	6.35	│ │
G	5	*vulgar*	31.26	│ │ │	J	17	*vulgar*	6.48	│ │
J	17	*vulgar*	31.67	│ │	G	5	*vulgar*	6.50	│ │
F	9	*nivali*	31.89	│ │	F	9	*nivali*	6.62	│ │
I	6	*boccam*	32.53	│ │	I	6	*boccam*	6.65	│ │
M	2	*boccam*	33.66	│ │ │	N	7	*vulgar*	6.94	│ │
N	7	*vulgar*	34.09	│ │	L	9	*vulgar*	7.12	│ │
L	9	*vulgar*	34.29	│	M	2	*boccam*	7.12	│ │
O	4	*boccam*	35.08	│	O	4	*boccam*	7.17	│
P	11	*iberic*	35.25	│	P	11	*iberic*	7.34	│
Q	8	*subpal*	43.56		Q	8	*subpal*	8.91	
		MW					ZW		
B	5	*eskimo*	12.91	│	B	5	*eskimo*	13.84	│
A	10	*rixosa*	13.33	│	E	5	*pygmae*	14.16	│ │
E	5	*pygmae*	13.47	│ │	A	10	*rixosa*	14.18	│ │
H	16	*vulgar*	13.69	│ │	H	16	*vulgar*	14.82	│ │ │
C	4	*allegh*	13.76	│	C	4	*allegh*	14.90	│ │ │
F	9	*nivali*	13.97	│	G	5	*vulgar*	15.28	│ │ │
G	5	*vulgar*	14.02	│	D	2	*campes*	15.48	│ │ │ │
D	2	*campes*	14.03	│	K	15	*vulgar*	15.51	│ │ │ │
K	15	*vulgar*	14.13	│	F	9	*nivali*	15.53	│ │ │ │
J	17	*vulgar*	14.55	│	I	6	*boccam*	15.85	│ │ │
I	6	*boccam*	14.90	│	J	17	*vulgar*	15.94	│ │
L	9	*vulgar*	15.39	│ │	M	2	*boccam*	17.16	│ │ │
N	7	*vulgar*	15.69	│ │	L	9	*vulgar*	17.17	│ │
M	2	*boccam*	15.90	│ │	N	7	*vulgar*	17.30	│ │
O	4	*boccam*	16.31	│	O	4	*boccam*	17.54	│
P	11	*iberic*	16.40	│	P	11	*iberic*	18.03	│
Q	8	*subpal*	21.62		Q	8	*subpal*	23.47	

Table 6. **First two standardized canonical vectors from the discriminant function analysis of four cranial variables from *Mustela nivalis* females**
Numbers in parentheses represent the percentage of the variance of each variable contributed to the canonical vector

Variable	Standardized canonical vectors 1	 2	Cumulative percent
1. CBL	0.411 (88.38)	1.092 (9.34)	97.72
2. IOW	−0.445 (93.61)	0.898 (5.72)	99.33
3. MW	0.441 (87.24)	−1.175 (9.27)	96.51
4. ZW	0.559 (93.52)	−0.486 (1.06)	94.58
Percent trace	92.27	5.47	
Cumulative percent		97.74	

Test of equality of group centroids: $F = 6.190$ with 64 and 452 degrees of freedom. $P < 0.0001$.

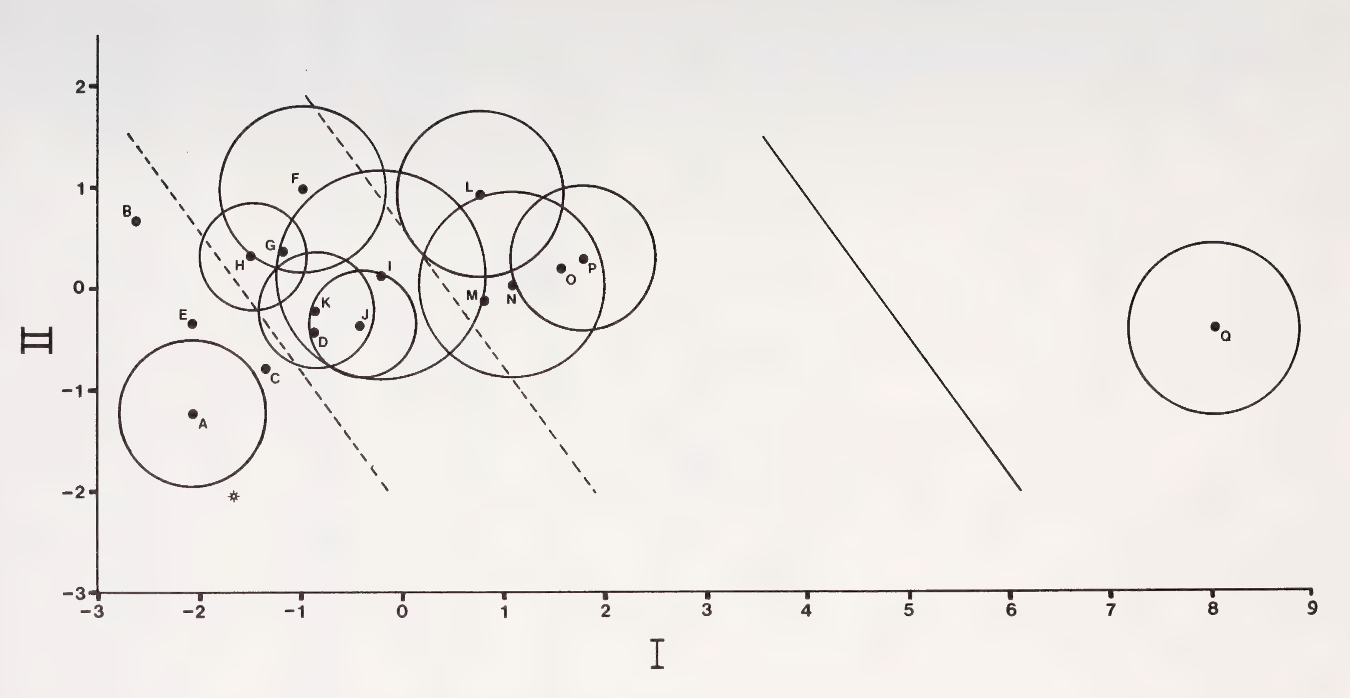


Fig. 6. Canonical graph showing the centroids and respective 95 % confidence circles of 17 geographic samples of female *Mustela nivalis.* No confidence circles for samples of less than six specimens were calculated. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*allegheniensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Northern Europe (*nivalis*); G: Southern Germany (*vulgaris*); H: Switzerland (*vulgaris*); I: Balkan Peninsula (*boccamela*); J: Northern Germany (*vulgaris*); K: Central and Western Germany (*vulgaris*); L: Western Europa (*vulgaris*); M: Southwestern Asia (*boccamela*); N: Silesia (*vulgaris*); O: Italy (*boccamela*); P: Iberian Peninsula (*iberica*); Q: Egypt (*subpalmata*). The asterisk represents a single specimen of *M. n. russelliana* from Szechwan, scored a posteriori

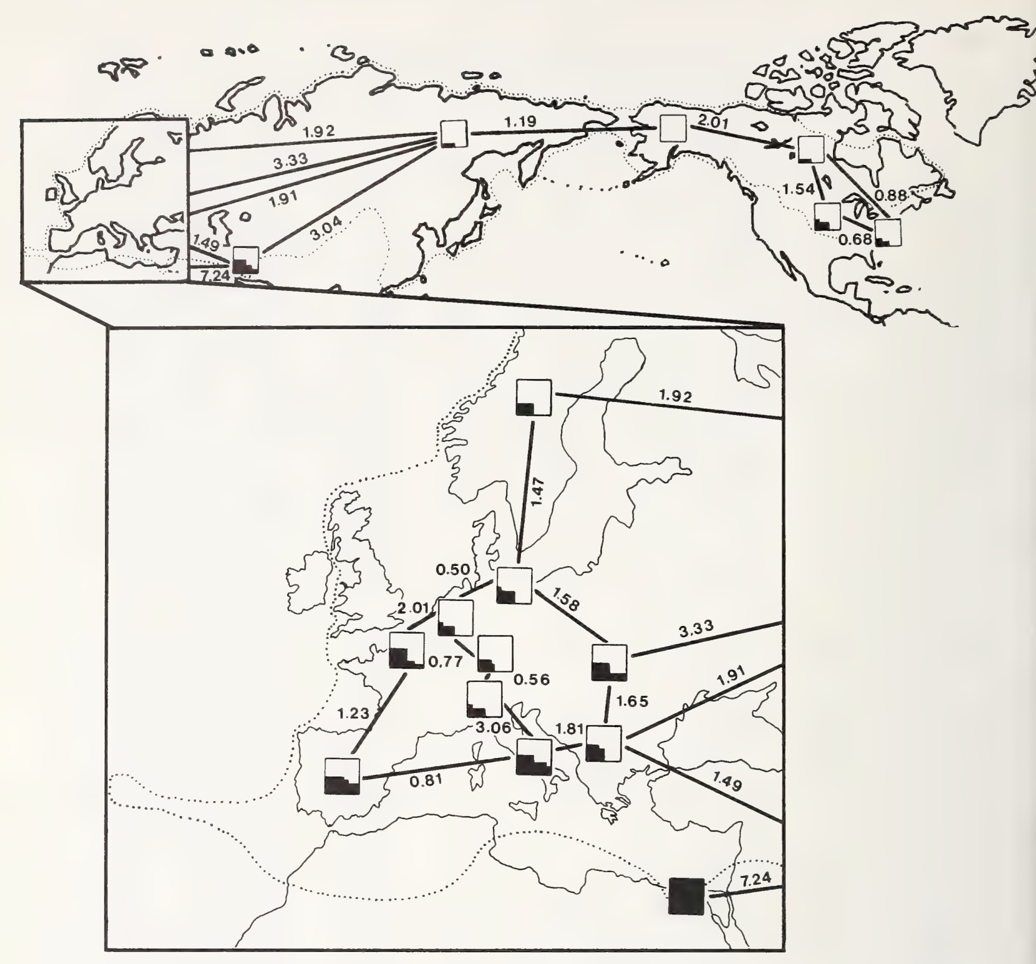


Fig. 7. Geographic variation in the skulls of female *Mustela nivalis.* In North America and Asia from east to west: Eastern U.S. (*allegheniensis*); Central great plains (*campestris*); Canada (*rixosa*); Alaska-Yukon (*eskimo*); Eastern Siberia (*pygmaea*); Southwestern Asia (*boccamela*). In Europe and North Africa, from north to south and east to west: Northern Europe (*nivalis*); Northern Germany (*vulgaris*); Central and Western Germany (*vulgaris*); Silesia (*vulgaris*); Southern Germany (*vulgaris*); Western Europe (*vulgaris*); Switzerland (*vulgaris*); Balkan Peninsula (*boccamela*); Italy (*boccamela*); Iberian Peninsula (*iberica*); Egypt (*subpalmata*). Further details as in Fig. 4

Discussion

The results of the craniometric analyses presented above support the view that all Holarctic weasels of the taxa included in this study are members of one variable species, with the notable exception of *subpalmata.* The latter taxon differs both morphometrically and with respect to sexual dimorphism of size from all the other taxa. These differences suggest the possible existence of underlying genetic and/or epigenetic mechanisms in *subpalmata* that differ from those in the other taxa. There is thus sufficient evidence to suspect that *subpalmata* may have evolved independently for a considerable period of time and may be specifically distinct from *M. nivalis.* This requires confirmation from the study of other character sets, including molecular data.

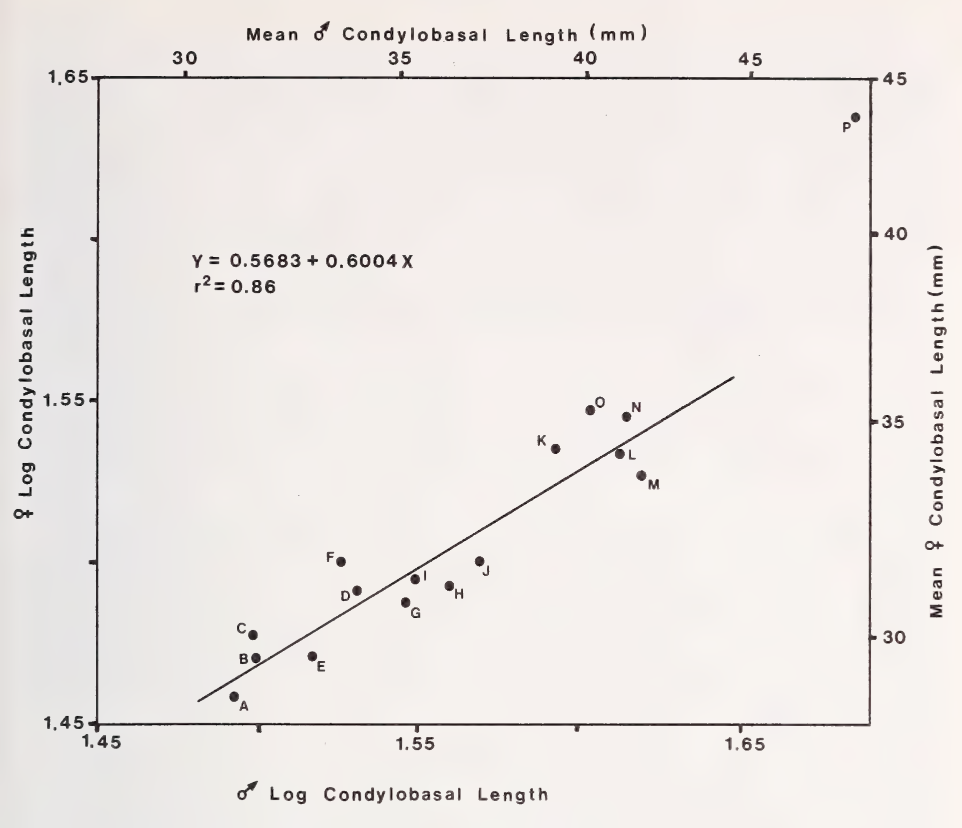


Fig. 8. Sexual dimorphism of size in *Mustela nivalis.* The equation describes the linear relationship between size of males and of females in populations of *M. nivalis* (without *subpalmata*) varying in size from small to large; r^2 is a measure of goodness of fit. A: Canada (*rixosa*); B: Alaska-Yukon (*eskimo*); C: Eastern U.S. (*allegheniensis*); D: Central Great Plains, U.S. (*campestris*); E: Eastern Siberia (*pygmaea*); F: Northern Europe (*nivalis*); G: Switzerland (*vulgaris*); H: Central and Western Germany (*vulgaris*); I: Southern Germany (*vulgaris*); J: Northern Germany (*vulgaris*); K: Western Europa (*vulgaris*); L: Silesia (*vulgaris*); M: Southwestern Asia (*boccamela*); N: Italy (*boccamela*); O: Iberian Peninsula (*iberica*); P: Egypt (*subpalmata*)

All other taxa in this study represent overlapping gradations in morphology and share a common sexual size dimorphism. Both, morphology of the skull and the difference in size between the sexes, are predominantly effectuated by overall size. The conclusion is that these taxa constitute one species, *M. nivalis.* The results of the morphometric analysis do not agree with the great number of subspecies recognized in the literature and suggest that a reduced number would be more realistic. A complete taxonomic revision, using all available characters and maximum geographic representation, is indicated. Such a revision clearly lies outside the scope of the present study. However, the results of this analysis support a breakdown of the populations studied into three subspecific groups: 1. The *nivalis* group. A group of small weasels, characterized by white winter pelage and distributed throughout the northern coniferous biome of Eurasia and North America. 2. The *vulgaris* group (including *boccamela* and *numidica*). A group of intermediate to large sized weasels, characterized by brown winter pelage and distributed in the temperate deciduous biome and Mediterranean region of the western Palearctic region. 3. A Central Asian group of intermediate sized weasels *(pallida),* with white winter pelage (HEPTNER et al. 1974).

This represents a reduction in the number of taxa distinguished by Frank (1985) in the western Palearctic. As Frank (1985) pointed out, and the results of this study confirm, *vulgaris* and *boccamela* are difficult to delineate. Populations designated to these subspecies form a gradual north-south cline, lacking the marked morphological discontinuity that characterizes the transition between *nivalis* and *vulgaris.* They are, therefore, best combined into one taxonomic category. The existence of a *numidica* group, postulated by Frank (1985) as being an independent species (type locality: Tangiers, Morocco) most closely resembling the ancestor of least weasels, is not supported by the morphometric evidence. The northwest African sample is morphometrically not distinct from other Mediterranean weasels (it is closest to samples from the Balkan [D = 0.92] and Italy [D = 1.81]). It seems, therefore, likely that *M. nivalis* invaded North Africa via Spain during the late Pleistocene, like other Palearctic elements. The weasel from Crete (*galianthas*), one of the insular forms included in the presumed ancestral *numidica* group by Frank (1985), is represented by one specimen. It was scored and plotted a posteriori (Fig. 3) to gain some idea about its possible affinities. Its position indicates that it is similar to other forms from the Mediterranean area and closest to the topotypic sample of *boccamela* from Sardinia. The time of isolation of the northwest African and island populations in the Mediterranean from those on the European mainland may be comparable to that of the eastern Siberian and North American populations. The respective morphometric differences are approximately of the same magnitude, a consideration that lends some support to this assumption.

The small Central Asian sample is from one locality (Dzharkent = Panfilov) in east Kazahkstan. More samples from central Asia will have to be studied before a clear picture of geographic variation in the area can emerge. A single specimen from Szechwan is similar to the boreal Asian and North American forms (Fig. 6), which suggests that the species entered China from the north.

The great variation of the species in the western Palearctic and the fossil record (Kurtén 1968) suggest that *M. nivalis* evolved here. It appears highly likely that the small northern forms (*nivalis*) evolved most recently, under the prevailing boreal conditions of the Pleistocene glaciations. Their adaptations to boreal conditions having been perfected, they subsequently spread east throughout northern Asia, invading North America only during the late Pleistocene.

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Zusammenfassung

Morphometrische Analyse der Schädelvariation beim holarktischen Mauswiesel (Mustela nivalis)

Die Schädelvariabilität der Mauswiesel (*Mustela nivalis*) aus verschiedenen Teilgebieten des holarktischen Artareals wurde morphometrisch untersucht. Schädelmaße erwachsener Tiere wurden multivariaten Diskriminanzanalysen unterzogen, um eine Klärung in der Systematik der Mauswiesel herbeizuführen. Die Ergebnisse dieser Analysen zeigen, daß die Populationen verschiedener Teilgebiete, außer die ägyptische (*subpalmata*), einem morphologischen Kontinuum angehören und hauptsächlich in der Größe variieren. Diese Beobachtung stützt die Behauptung, daß diese Populationen einer Art zuzuordnen sind. Die morphometrischen Daten ermöglichen eine Teilung in drei phänotypisch ähnliche subspezifische Gruppen: die *nivalis*-Gruppe, kleine Wiesel der borealen Gebiete der Holarktis; die *vulgaris*-Gruppe, mittel- bis großwüchsige Wiesel, welche die gemäßigten und mediterranen Gebiete der westlichen Palaearktis bewohnen, und eine zentralasiatische Gruppe (*pallida*). Das ägyptische Wiesel ist wahrscheinlich eine selbständige Art.

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Some physical and population characteristics of Egyptian mongooses (*Herpestes ichneumon* L., 1758) in southwestern Spain

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Abstract

Studied physical and population characteristics of Egyptian mongooses, *Herpestes ichneumon*, in southwestern Spain using trapping and radio-tracking. Males and females differed (p = 0.04) in body mass (3142 and 2823 g, respectively). Females were more often trapped than males (1.8F:1M), and adult than young (1.8A:1Y). Copulations occurred mainly (63.6 %) in March and April, and births (77.8 %) in May, June and July. The mean number of cubs per litter was 2.7 ± 0.8 (N = 7). Density for adult individuals was estimated as 1.2 ind./km^2. Annual survival rates were very low, oscillating between 0.13 in 1988/89 for adults and the same figure in 1987/88 for young, and 0.6 in 1987/88 for adults. After two years, life expectancy did not exceed 3 %. Of 16 dead mongooses, only 6.3 % were due to natural causes (predation), 25 % unknown, and the remainder from human activities, both direct (illegal hunting) and indirect (road kills).

Introduction

Egyptian or large grey mongoose, *Herpestes ichneumon*, is the only herpestid (Wozencraft 1989) with free-ranging populations in Europe (Corbet 1984; Carpaneto 1990), where its distribution is limited to the southwestern quadrant of the Iberian Peninsula. At the end of the last century it occurred in northwestern regions of Spain as well (Delibes 1982). The species is included in the Spanish Vertebrate Red Data Book, where its status is considered "unknown" (Icona 1986).

Except for some general data (Valverde 1960, 1967), and studies on its diet (Delibes et al. 1984; Palomares and Delibes 1991a, 1991b) and distribution (Delibes 1982), the biology and ecology of the Egyptian mongoose in Europe remain unknown. Recently, radio-tracking studies on time budget and spacing have been carried out in Doñana National Park (Beltrán et al. 1985; Delibes and Beltrán 1985; Palomares 1990; Palomares and Delibes 1991c). Here we describe some aspects of the physical and population characteristics of Egyptian mongooses in Doñana, including body mass, external measurements, sex and age proportions, reproduction, density, survival rates, and causes of mortality.

Material and methods

Trapping of mongooses and marking with radio-collars were carried out from September 1987 to September 1989 at Coto del Rey (Northern Doñana National Park, SW Spain, approx. 37°9′ N 6°26′ W) (Palomares 1990). Coto del Rey is almost completely reforested by pines, *Pinus pinea*, and eucalyptus, *Eucalyptus* sp., with undergrowth mainly of *Halimium halimifolium*. Small natural streams, where *Fraxinus* sp., *Populus alba, Pistacia lentiscus* and *Rubus* sp. grow, also occur. Patchily distributed over the area, associations of *Lentiscus* are found at sites with a higher water table. The climate is subhumid Mediterranean, characterized by dry, hot summers and wet, mild winters. The

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terrain is flat and the soil is sandy. For more information about the study area, see VALVERDE (1958) and RIVAS-MARTÍNEZ et al. (1980).

Captured animals were sexed, weighed, and aged according to tooth wear (adults, with definitive and completely developed teeth; immatures, with definitive teeth, but with some teeth still growing; and young, with one milk tooth or more). The following body measurements were taken for every animal: head-body length, tail (terminal hairs not included) length, hilt height, hind-foot length and ear length.

Birth dates were obtained by estimating the age of the young individuals from body mass, head-body length and tail length when trapped, following BEN-YAACOV and YOM-TOV (1983). Courtship and copulation dates were estimated by direct observations from radio-collared individuals, and from data of birth dates, assuming a gestation period of 60–70 days (KINGDON 1977; BEN-YAACOV and YOM-TOV 1983). The number of cubs per birth was obtained from observation of family groups with at least one radio-collared individual, and by examining two pregnant females. Additionally, information on copulations, births, and litter size obtained in other sites in southern Spain and from captive individuals between 1973 and 1977 is also included.

Density was estimated from radio-tracking data of adult individuals. It was based on home range size and the percentage of overlap of the minimum area (minimum convex polygon method) where the trapping was undertaken (or trapping area; see MCLELLAN 1989, for a description of method). Since most mongooses were caught and tracked in 1988–89, we use the data from this period, although they are completed with those of the previous year (since home ranges seemed very stable although its dwellers changed; PALOMARES 1990). The home range of each individual was estimated by use of the minimum convex polygon method (MACDONALD et al. 1980), using only animals localized for 20 or more isolated times (time between locations was at least 4 hours; SWIHART and SLADE 1985; REYNOLDS and LAUNDRÉ 1990).

Rates of survival (annual and total for the two study years, for both adult and young, immatures included) were estimated from daily survival for the tracking period using MICROMOR program (HEISEY and FULLER 1985). Radio-collared mongooses and untagged animals frequently sighted together, were included in the analysis. Causes of death were determined from autopsy. The annual period to estimate survival rates of the young (see HEISEY and FULLER 1985) was early July to early February, the only period in which they were sighted and trapped in the study area (PALOMARES 1990).

Results

Physical characteristics

Only body mass was significantly different between males and females (means of 3142 g and 2823 g, respectively; p = 0,04, "t" test; Tab. 1). No other difference was significant ($p > 0.05$), although males appeared to be larger (Tab. 1).

Sex and age rates

Of 25 captured mongooses 9 were males and 16 females (1M:1.8F); the ratio did not differ significantly from equality ($\chi^2 = 1.960$, $p = 0.162$; Exact Test of WELLS and KING 1980). A

Table 1. **Mean and standard deviation (SD) of body mass (g) and external measurements (mm) of adult male and female Egyptian mongooses caught from September 1987 to September 1989 in Doñana National Park**

The "t" test and probability (p) values for comparisons of traits between sexes are given

	Mass[a]		Head-body[a]		Tail-base[a]		Hilt[a]		Back foot[a]		Ear[b]	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Males	3142.2	376.2	526.7	25.0	449.6	24.3	212.9	28.3	86.9	15.3	34.4	2.6
Females	2823.3	177.4	529.7	19.8	433.3	23.7	210.8	17.2	90.6	2.8	33.9	2.2
"t"	2.354		0.297		1.530		0.193		0.716		0.409	
p	0.040		0.771		0.144		0.851		0.495		0.689	

[a] N = 9 and 12 for males and females, respectively. – [b] N = 8 and 11 for males and females, respectively.

higher proportion of females was found in both young-immature (3M:6F) and adult (6M:10F) individuals. None of these proportions differed significantly from the expected 1:1 ratio (χ^2 = 0.78 and 0.51, p = 0.622 and 0.722, respectively), possibly due to small sampling size.

Young were trapped less often than adults (7 young, 2 immature and 16 adults; 1:1.8 between non-adults and adults). This proportion most likely changes throughout the year, since, as suggested by trapping data, the young grow quickly and can hardly be differentiated from adults at 9–12 months of age (PALOMARES 1990).

Reproduction

Courtship and copulation took place from early February to early June, with the peak frequency (63.6 %) in March and April, and births from mid April to mid August, with the peak frequency (77.8 %) from May to July (Figure). VALVERDE (1967) observed two births in July and August. In captivity copulation was observed in January, March, April, May, June and October (Figure).

COPULATION

BIRTH

JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV

MONTH

Copulation and birth dates of Egyptian mongooses in Spain. Black circles = data obtained during field work of this study; open circles = observations obtained in captivity; asterisks = data from VALVERDE (1967)

The numbers of cubs observed in four family groups were 2, 3, 3, and 2. In two pregnant females 3 and 4 foetuses could be detected. On the other hand, a captive female gave birth to 2 cubs, and another had 3 foetuses. In total, the mean number of cubs per birth was 2.7 ± 0.8.

Density

Nine adult mongooses inhabited their entire or partial home range in the trapping area between January and August of 1989. However, the number of locations for a male was insufficient for estimating home range size, and this information was replaced by the data of another adult male, which occupied the same space one year previously. The total number of localizations for 3 males and 6 females was 807 (mean = 89.7, SD = 80.0, range = 20–259). Mean individual percentage of home range overlapping with the trapping area was 34.4 % (SD = 16.6, range = 4.0–61.4). Estimated density of adult mongooses was 1.2 ind./km^2. If we consider the above-estimated proportions of young and immature individuals in the population, the total density would be near 2 ind./km^2.

Causes of mortality and survival rates

Twenty-four of 25 trapped mongooses were equipped with radio-collars. Of these, one adult female was shot, one young female was killed by a dog, *Canis lupus* f. fam., or lynx, *Felis pardina,* and one adult male was caught in a poacher's foot-trap. The radio-collars of 3 other adult females, stopped sending, probably due to death of the animal. At least once, local people said that they had been killed by poachers. Of 5 mongooses not equipped with radio-collars but used to stay with a radio-collared animal, 4 might have died: two cubs of the shot female, and the other two which were no longer observed after a poacher had set foot-traps in their core areas.

Although in most cases confidence intervals are wide, annual survival rates were very low, oscillating between 0.13 in 1988/89 for adults and the same figure in 1987/88 for young, and 0.6 in 1987/88 for adults (Tab. 2). For adults, differences between years were significant ($Z = 2.03$, $p = 0.0212$). After two years, life expectancy did not exceed 8 % for both the adults and young (Tab. 2).

Table 2. **Numbers of individuals controlled (NC), deaths (ND) and survival rates of adult and young Egyptian mongooses in Coto del Rey during each study year**

95 % confidence limits are shown in parentheses. Number of days/mongoose for each period and age class was 592 and 707 in adults, and 209 and 426 in the young, for 1987/88 and 1988/89, respectively

	NC	ND	Survival
Adults			
1987/88	6	1	0.60 (0.22–1.0)
1988/89	11	4	0.13 (0.02–0.95)
Total	17	5	0.08 (0.01–0.73)
Young			
1987/88	4	2	0.13 (0.01–1.0)
1988/89	8	3	0.22 (0.04–1.0)
Total	12	5	0.03 (0.0 –0.78)

We have additional data since December 1985 on mortality of six mongooses from other locations in Doñana National Park. From 16 dead mongooses, 2 died in foot-traps, 2 others in road kills, 1 was captured in a snare, 1 was shot and 10 died from unknown causes. The last category includes 2 shot female cubs, and 2 young and one adult female most likely trapped by poachers. Accepting the evidence as valid, at least 56.3 % of these deaths were caused by illegal hunting, 12.5 % by indirect human action (road kills), 25 % by unknown causes, and only 6.3 % by natural causes (predation).

Discussion

Mongooses of Doñana have greater body mass than individuals trapped throughout southern Spain and Israel, and in both places body mass was significantly different for each sex (Ben-Yaacov and Yom-Tov 1983; Delibes et al. 1984). In Israel (the only country with data), head-body length was also significantly different between males and females.

Females were more often trapped than males; however, this situation is rare in carnivores (e.g., Gorman 1979; Buskirk and Lindstedt 1989, for a review in mustelids; Fuller 1989; Hellgren and Vaughan 1989). This result is usually attributed to the greater movements and larger home ranges of males, which are thus more inclined to enter traps (see Buskirk and Lindstedt 1989). Male mongooses had, as a rule, larger home ranges than females, and a higher number of core areas (Palomares 1990). This should have produced a higher probability of capture which, however, was not found. Since more young females than males (both roaming in family group; Palomares 1990) were also trapped, perhaps an unequal sex ratio could be the cause. Nevertheless, the spacing system of mongooses (with several females inside the territory of an adult male; Palomares 1990) could produce a reversed proportion is less favourable areas, where the males searching for an unoccupied territory would superabound. In captures in Cádiz country (southern

Spain) more males than females (30M:11F) occurred (Delibes, unpubl.). Adding the data of Doñana to the last mentioned site, the sex ratio is 1M:1F (N = 66).

Copulation and birth dates, and offspring size obtained in this study, are similar to data presented by Dücker (1965) for captive individuals. Nevertheless, with our method to calculate offspring size there is no guarantee for a lose of cubs, prior to observation dates. In fact, during the tracking period, a young was killed by a dog or lynx, and 2 others were lost under unusual circumstances (most likely killed by poachers), while still accompanied by their mothers. Birth dates overlap with yearly peaks of rabbit (*Oryctolagus cuniculus*) density (Beltrán 1991). Rabbits are the main prey of mongooses in this area (Palomares and Delibes 1991b).

Mongoose density outside the trapping area is lower than inside, since we studied the more favourable habitats and sites. On the other hand, a weak point of our method lies in the territoriality of the studied species and in the setting-up of the study-area boundaries. Both problems were solved by the home range exclusivity of mongooses in Doñana, especially males (Palomares 1990), and the determination of a "trapping area" according to McLellan (1989).

The lower survival rates and higher mortality due to human actions prove again that a National Park status is not sufficient guarantee of species conservation (Dasmann 1983), especially in the case of carnivores which need large home ranges and usually inhabit edges of protected areas (Ferreras et al. 1991). Only a high birth rate and immigration from other areas with lower mortality can explain the survival and the high relative density of the species in the study area.

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Zusammenfassung

Einige Daten zur Populationsbiologie des Ichneumons (Herpestes ichneumon L., 1758) in Südwest-Spanien

Eine Population des Ichneumons (*Herpestes ichneumon*) wurde über einen Zeitraum von zwei Jahren in Südwestspanien (Nationalpark Doñana) mit Hilfe von Fallenfängen und Radiomarkierung untersucht. Daten zu Körpergewicht und Größe, Geschlechtsproportionen, Altersstruktur, Fortpflanzung, Populationsdichte, Überlebensrate und Sterblichkeitsursachen werden mitgeteilt. Die Geschlechter unterscheiden sich nur im mittleren Gewicht (3142 g bei Männchen und 2823 g bei Weibchen). Weibchen fingen sich öfter in Fallen als Männchen, unabhängig vom Alter (1,8W:1M). Paarungen wurden hauptsächlich im März und April (63,6 %), Geburten im Mai, Juni und Juli (77,8 %) registriert. Die Wurfgröße betrug 2,7 ± 0,8 (N = 7). Die Populationsdichte für adulte Ichneumons wird auf 1,2 Ind./km^2 geschätzt. Die jährliche Überlebensrate war trotz breiter Konfidenzintervalle sehr niedrig; 0,6 (1987/88) und 0,13 (1988/89) für Adulte, und 0,13 (1987/88 für Jungtiere. Wenn beide Jahre miteinbezogen werden, dann überschreitet die Überlebensrate keine 3 %, sowohl bei Adulten wie bei Jungtieren. Die Mortalität von 16 aufgefundenen Tieren war in 6,3 % der Fälle auf natürliche Ursachen (Prädatoren) zurückzuführen; 25 % der Fälle bleiben ungeklärt, und in den übrigen Fällen waren entweder illegale Jagd oder der Straßenverkehr verantwortlich.

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Bacular variation in the subgenus *Trinomys*, genus *Proechimys* (Rodentia: Echimyidae)

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Abstract

Bacular morphology and variation in the four species of spiny rats of the subgenus *Trinomys*, genus *Proechimys* is described. Each species can be uniquely diagnosed on the basis of bacular morphology alone. *Proechimys dimidiatus* and *P. iheringi* have similar overall bacular morphology, although they differ noticeably from *P. setosus* and *P. albispinus*. The latter two species differ markedly in the morphology of the baculum.

Introduction

The spiny rats included in the subgenus *Trinomys* Thomas, genus *Proechimys* Allen, occur in eastern Brazil from the state of Bahia to the state of São Paulo. According to Moojen (1948) four species are recognized in the subgenus *Trinomys: P. dimidiatus* (Günther), *P. iheringi* Thomas, *P. setosus* (Desmarest), and *P. albispinus* (Geoffroy). These species can be diagnosed on the basis of a combination of traits that include the size, shape, and color of aristiform hairs, morphology of the skull, and pattern of cheekteeth counterfolds (Moojen 1948), although substantial overlap in the distribution of character states among the species makes identification a rather difficult task. To date there have been no studies of bacular morphology in the subgenus *Trinomys*. In this note we describe bacular morphology and variation in the four species of the subgenus *Trinomys*.

Material and methods

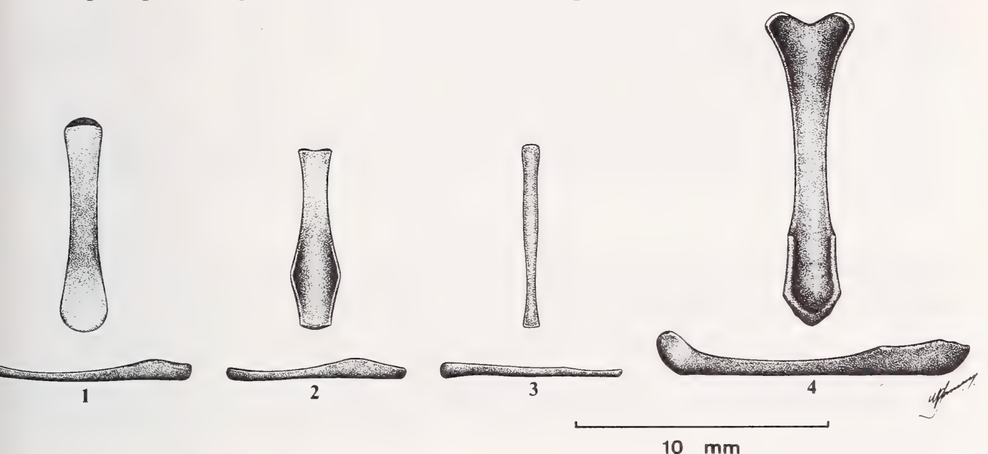
The specimens employed in this study were identified using a combination of pelage and skull traits described by Moojen (1948). Phalli were removed from skins of preserved specimens deposited in the mammal collection of the Museu Nacional (UFRJ) and immersed in water for 24 hours. Bacula were dissected from surrounding tissues under the binocular microscope. Only adult specimens, age classes 8–10 of Patton and Rogers (1983), were used in this study. The following samples were examined: *P. dimidiatus* (state of Rio de Janeiro: Tijuca [n = 5]); *P. iheringi* (state of Espírito Santo: Santa Teresa [n = 5]); *P. setosus* (state of Minas Gerais: Juiz de Fora [n = 2]), Peti [n = 1], Lagoa Santa [n = 1]); *P. albispinus* (state of Bahia: Jaguaquara [n = 1], Jequié [n = 4]).

Results and discussion

The baculum in the subgenus *Trinomys* is an elongate and narrow structure with a straight shaft (see Figure and Table). This structure varies, however, in the shape of the proximal and distal ends and in the development of the dorsoventral curvature. In *P. dimidiatus* the shaft does not show any development of a dorsoventral curvature but it has a lateral indentation near mid-shaft. The proximal and distal ends are evenly round, and the latter

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shows no development of apical wings or median depression. In *P. iheringi* the shaft has a slight dorsoventral curvature in the proximal third, and shows an indentation near the distal end. The distal end is slightly concave and has no apical wings or median depression. The shaft broadens near the proximal end and is tapered in the tip. The baculum in *P. setosus* does not show a dorsoventral curvature and has a lateral indentation near the posterior tip. The proximal and distal ends are nearly square. The proximal end is slightly paddle-shaped and the distal end has no apical wings or median depression. In *P. albispinus* the baculum has a dorsoventral curvature and slightly tapered lateral indentations near mid-shaft. The proximal end is paddle-shaped and pointed. The distal end has well developed apical wings with a pronounced median depression (Figure).



Ventral (A) and lateral (B) views of bacula of species of the subgenus *Trinomys*, genus *Proechimys*. The distal part is put to the top (ventral view) and left (lateral view). 1: *P. dimidiatus*, 2: *P. iheringi*, 3: *P. setosus*, 4: *P. albispinus*

Four measurements were taken from bacula of the four species and are shown in Table 1. *Proechimys dimidiatus, P. iheringi,* and *P. setosus* bacula are similar in greatest length of shaft (Table). These species are also similar in body size (Moojen 1948). On the other hand, *P. albispinus* has the smallest body size among the species of *Trinomys* (Moojen 1948) but it has the largest baculum.

Overall bacular morphology is similar in both *P. dimidiatus* and *P. iheringi* although their bacula differ noticeably from those of *P. setosus* and *P. albispinus*. The latter two species also differ markedly in bacular morphology. Moojen's (1948) assessment of specific variation in the subgenus *Trinomys* revealed several cranial characters shared by *P. dimidiatus* and *P. iheringi* and by *P. setosus* and *P. albispinus*. He actually implied a close morphological relationship between *P. dimidiatus* and *P. iheringi*. The morphological

Means and (standard deviations) for measurements taken from bacula of the four species of *Proechimys* of the subgenus *Trinomys*

Characters	Taxon			
	P. dimidiatus (n = 5)	*P. iheringi* (n = 5)	*P. setosus* (n = 4)	*P. albispinus* (n = 5)
Greatest length of shaft	7.6 (0.57)	6.7 (0.61)	7.4 (0.21)	11.4 (0.65)
Maximum width of proximal end	1.8 (0.19)	1.7 (0.15)	0.6 (0.10)	2.0 (0.05)
Maximum width of distal end	1.4 (0.19)	1.2 (0.13)	0.8 (0.06)	3.1 (0.29)
Least width of shaft	0.9 (0.12)	0.8 (0.11)	0.5 (0.00)	1.1 (0.15)

similarity found by MOOJEN (1948) for the latter species is indeed corroborated by bacular morphology. On the other hand, the similarity between *P. setosus* and *P. albispinus* established on the basis of cranial morphology (MOOJEN 1948) is not supported by bacular morphology.

PATTON (1987) recently reviewed morphological variation and systematics in the subgenus *Proechimys* and showed that the baculum can be either long and narrow or massively long and broad. PATTON (1987) also showed that bacular morphology in addition to skull morphology allowed the definition of nine groups of species in the subgenus *Proechimys*. We showed here that each species in the subgenus *Trinomys* can be uniquely diagnosed by the morphology of the baculum. We believe this is an important result because the degree of distinctiveness in bacular morphology among species of *Trinomys* is not matched by the amount of variation known to exist in the skull and pelage. The skull and pelage have traditionally been employed in the taxonomy of the subgenus *Trinomys*, but have not always allowed correct identification of taxa. It should also be pointed out that, whereas in the subgenus *Proechimys* the baculum can be useful to define groups of species (PATTON 1987), in the subgenus *Trinomys* this structure is diagnostic at the species level.

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Zusammenfassung

Baculumvariation im Subgenus Trinomys, Genus Proechimys (Rodentia: Echimyidae)

Morphologie und Variation von Bacula werden für 4 Arten von Stachelratten des Subgenus *Trinomys*, Genus *Proechimys* beschrieben. Danach kann jede Art eindeutig diagnostiziert werden. Dennoch sind die Bacula von *Proechimys dimidiatus* und *P. iheringi* einander in Form und Ausmaßen ähnlicher, gegenüber denen von *P. setosus* und *P. albispinus* jedoch deutlich verschieden.

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Postnatal development of three sympatric small mammal species of southern Africa

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Abstract

Four species of small mammals occur sympatrically in an arid area of the southwestern Cape Province. Females of all four species produced young after capture during a field excursion in September 1990. Postnatal development of three species, namely *Tatera afra, Acomys subspinosus* and *Elephantulus edwardii*, is reported for the first time, and compared with recorded data for the fourth species, *Aethomys namaquensis.*

T. afra produced altricial, nipple-clinging young, while young of *E. edwardii* were precocial and did not nipple-cling. *A. subspinosus* produced semi-precocial young which grew rapidly. Young of *A. namaquensis* are reported to be altricial, but the level of development at birth is more advanced than that of *T. afra.*

Differences in habitat and body size cannot account for the different life-history styles of these four species. Congenerics of each species included in this study exhibit similar life-history styles, with the exception of *Acomys* species, and it is suggested that altriciality/precociality is a phylogenetically conservative character in small mammals.

Introduction

Many theories have attempted to explain differences in life history styles of mammals (Perrin 1989). Adult body size, environment and phylogeny are just three of the factors which have been implicated in the selection of particular life history styles in animals. Western (1979) found that gestation time, growth rates, age at first reproduction, lifespan, birth mass and litter mass are all allometrically scaled to adult mass in mammals. Neal (1990) reviewed pre- and postnatal growth and development of 29 genera of African muroid rodents. He found that adult body mass had a strong influence on birth mass, gestation time, foetal growth rate, postnatal growth rate and litter growth rate. There was little evidence for phylogenetic effects on developmental parameters.

Stearns (1983) and Creighton and Strauss (1986) agree that most parameters of postnatal development of mammals scale to adult body size, but there appear to be phylogenetic constraints on the evolution of life-histories, and these differ from lineage to lineage.

The role of environment in selection of life history styles has been reviewed by Sibly and Calow (1985). Environmental conditions may determine the growth rates of offspring and age-specific survivorship, but internal constraints and trade-offs also influence life history strategies (Sibly and Calow 1985). Burda (1989) found no correlation between length of postnatal development and habitat, diet, social structure, climate, or ability/inability to vary metabolic rate in several rodent taxa.

The present study arose as a result of a field excursion to the Niewoudtville district of the Cape province. This area falls within the Western Mountain Karoo vegetation type (Acocks 1988). Very little soil covers the stony ground, which consists of shale, fine-grained sandstone and granite. Mean annual rainfall is less than 150 mm, most of which

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falls in winter. Vegetation consists of little grass and small, widely-scattered bushes (Acocks 1988).

Three rodent species of the subfamilies Gerbillinae (*Tatera afra*) and Murinae (*Acomys subspinosus, Aethomys namaquensis*) and one macroscelid species, *Elephantulus edwardii,* were trapped on the farm Sewefontein, and females of all species produced young after capture. Postnatal development of three species, *T. afra, A. subspinosus* and *E. edwardii* has not been recorded previously. Thus an opportunity was provided for recording the postnatal development of these species, and for comparing the development of four sympatric species of different genera and different body size.

Materials and methods

Five female *Elephantulus edwardii*; 4 female *Tatera afra*; 3 female *Acomys subspinosus*; and 4 female *Aethomys namaquensis* were live-trapped between 13. and 15. September 1990.

Individuals were caged singly after capture and returned to the animal house at the University of Natal, Pietermaritzburg. *E. edwardii* were housed in 60 × 30 × 30 cm glass terrain; all other species were kept in laboratory rodent cages. Rodent species were fed a mixture of seeds and rat cubes, supplemented with carrots, greens and insects. *E. edwardii* were fed "Pronutro", insects and sunflower seeds.

Young were weighed on a Sartorius U6300 balance, correct to 0.1 g, and hindfoot measurement was taken correct to 0.1 mm as an index of physical growth. Measurements commenced at birth–1 day old, and were taken at intervals of 1–3 days until young were 40–50 days old.

Postnatal growth rates were calculated for the relatively linear phase of increase in mass and hindfoot length (Case 1978). Growth rate was calculated as $\frac{mE - mB}{t}$ where mE = measurement at end of growth phase; mB = measurement at birth; t = time in days from birth to end of linear growth phase. Average growth curves were constructed by calculating mean mass and hindfoot length of all young in each 2-day age class.

Physical development was assessed on the days of weighing. Developmenal criteria used in assessing the level of physical development were as follows: ear pinnae folded down and attached to the head or folded back and free of attachment, lower or upper incisors erupted, eyes open or closed, degree of hair proliferation (a dark pigmentation of the skin was taken to represent the beginning of hair proliferation), toes fused or separate. The ages at which young were first attached to and spontaneously detached from the nipples were recorded, if nipple-clinging occurred. Weaning was judged to have begun when young were first seen eating solid food, and was complete when young were no longer suckled.

Results

The number of litters for each species, litter sizes, and longest interval between capture and birth of young are shown in Table 1. All females of the species *T. afra, A. subspinosus* and *E. edwardii* were pregnant when captured. In addition, three out of four *Aethomys namaquensis* gave birth to 3, 4 and 4 young within 2 weeks of capture.

Growth curves for mass and hindfoot length of *T. afra, E. edwardii* and *A. subspinosus* are shown in Figs. 1 and 2. The postnatal development of *Aethomys namaquensis* has been described previously (Neal 1990), and is not included in the present study.

Table 1. **Numbers of litters, litter sizes, and longest interval from capture to birth of young of *T. afra, A. subspinosus* and *E. edwardii***

	T. afra	*A. subspinosus*	*E. edwardii*
Number of litters	4	3	5
Litter sizes	3, 4, 4, 5	3, 3, 3	2, 2, 2, 2, 1
Longest capture-Birth interval	18 days	27 days	30 days

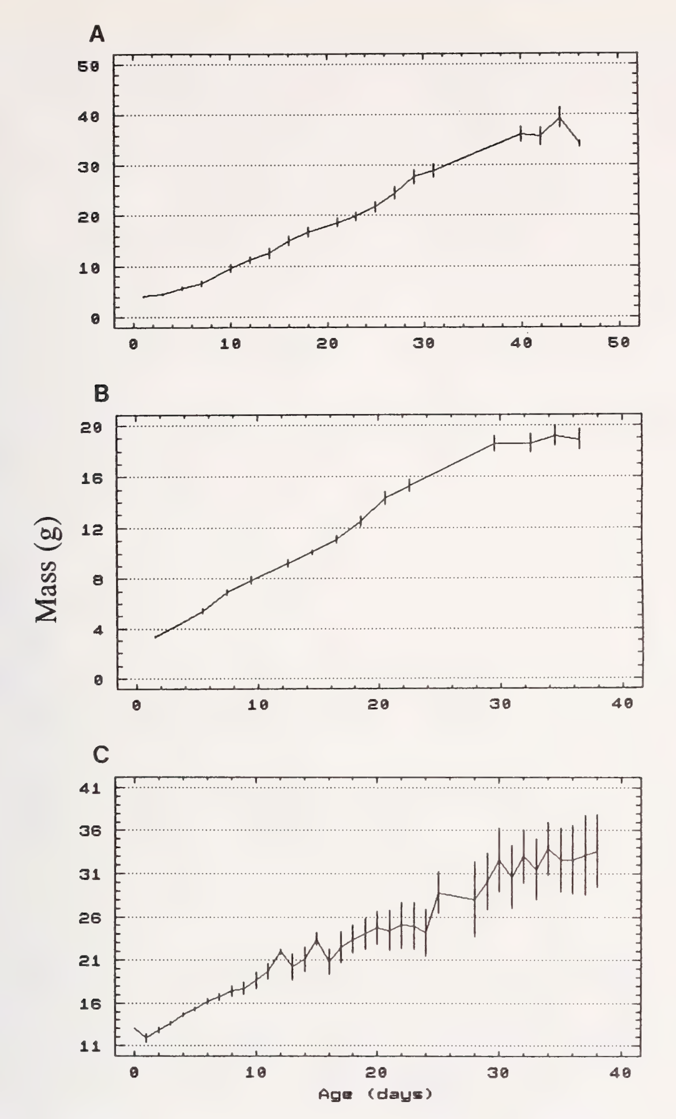


Fig. 1. Mean mass (± s.e.) of A: *Tatera afra,* B: *Acomys subspinosus,* C: *Elephantulus edwardii*

Body dimensions, growth rates, and timing of physical developmental parameters are shown in Table 2. Results show a clear difference in level of development at birth among the neonates of the three species. *T. afra* neonates were small relative to adult mass, *A. subspinosus* neonates were larger relative to adult mass than *T. afra*, and *E. edwardii* neonates were the largest relative to adult mass. When mean litter mass relative to adult mass was considered, *T. afra* still had the smallest litter mass (17.3 % of adult mass), while *A. subspinosus* and *E. edwardii* had litter masses of 46.5 % and 42.5 % of adult mass, respectively.

Growth rates in mass and hindfoot length were most rapid for *T. afra*, although at 30 days of age, young of this species had achieved only 30 % of adult mass and 78 % of adult hindfoot length. *A. subspinosus* had reached 87 % of adult mass at 30 days old,and 94 % of

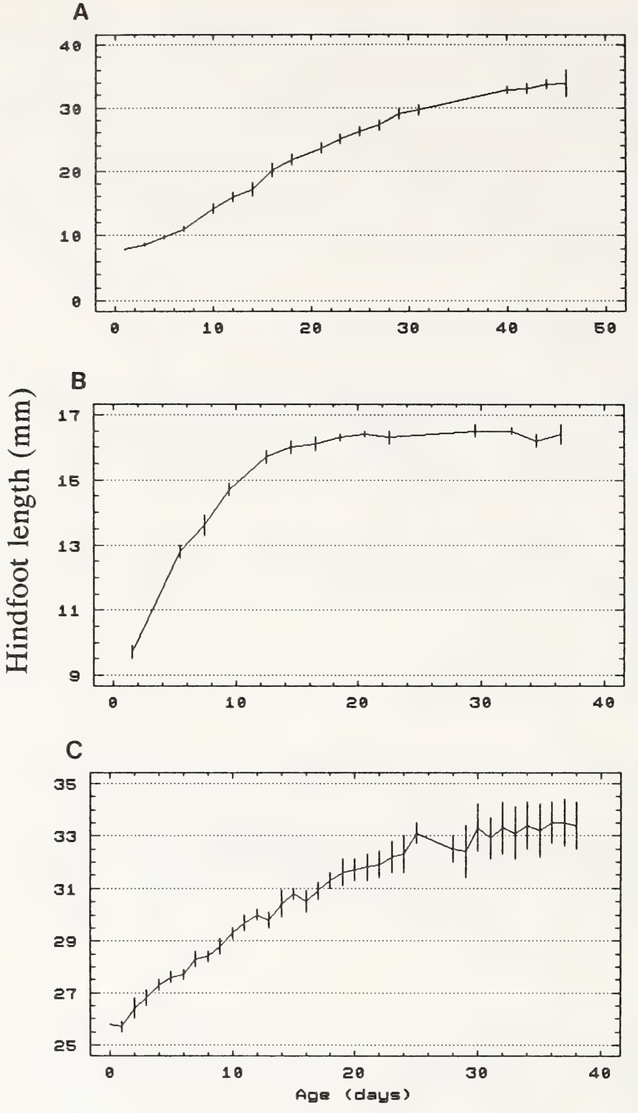


Fig. 2. Mean hindfoot length (± s.e.) of A: *Tatera afra,* B: *Acomys subspinosus,* C: *Elephantulus edwardii*

adult hindfoot length after only 16 days. *E. edwardii* had reached 65 % of adult mass and 95 % of adult hindfoot length by 30 days of age.

Physical development proceeded at different rates in the three species. *T. afra* neonates were hairless, unable to crawl effectively, blind, and had toes fused and ear pinnae fused to the head. Hair began to emerge from approximately 7 days of age, at which time the ear pinnae became detached from the skin of the head. Young were firmly attached to the nipples and were dragged with the mother when she moved. Incisors emerged at about 10 days and a groove was noticed between the two lower incisors. Eye-opening was recorded at 18–21 days, and shortly after this, young were seen detached from the nipples, eating solid food, and moving freely away from the nest.

A. subspinosus neonates were also naked and blind at birth, but hair was visible 1–2 days after birth, ear pinnae were free, and toes were separated within 2 days of birth. Nipple-clinging was not observed in *A. subspinosus.* Incisors erupted at approximately 7 days, and eyes opened at 9–10 days, at which time young were able to walk efficiently.

E. edwardii neonates were fully furred at birth, with eyes open, incisors erupted, ear pinnae free and toes separated. They were first observed eating solid food at 12–16 days. Nipple-clinging did not occur in this species, and neonates were fully mobile from birth.

Table 2. **Summary of body dimensions, litter, size, growth rates, and timing of certain developmental features in *T. afra, A. subspinosus* and *E. edwardii***

Characteristic	*T. afra*	*A. subspinosus*	*E. edwardii*
Adult body mass[a] (g) x̄	95.0 (n = 15)	21.3 (n = 26)	50.4 (n = 16)
Range	78–113	17–25	36–65
Birth mass ± s.e.	4.1 ± 0.1 (n = 13)	3.3 ± 0.1 (n = 6)	11.9 ± 0.5 (n = 5)
Birth mass % adult mass	4.3 %	15.5 %	23.6 %
Litter size	4.0 (n = 4)	3.0 (n = 3)	1.8 (n = 5)
Litter mass % adult mass	17.3 %	46.5 %	42.5 %
Growth rate (g/day)	0.82	0.55	0.59
Linear growth phase	0–43 days	0–28 days	0–38 days
Adult hindfoot (mm) x̄	37.7 (n = 15)	17.0 (n = 26)	34.6 (n = 16)
Range	28–40	13–19	33–36
Birth hindfoot ± s.e.	7.9 ± 0.1	9.7 ± 0.2	25.7 ± 0.2
Birth % adult hindfoot	21.0 %	57.0 %	74.3 %
Growth rate (mm/day)	0.64	0.55	0.30
Linear growth phase	0–39 days	2–13 days	1–25 days
Age (days) at development			
Ear pinnae free	6–7	0–1	0
Dorsal hair	6–8	1	0
Ventral hair	12	1	0
Toes separated	10–16	0	0
Incisors erupt	10	7	0
Eyes open	20	9–10	0
Attached to nipples	1–3	–	–
First unattached	22–24	–	–
Efficient walking	24	9–10	0
Eat solid food	22–23	?	12–16

[a] Data from Skinner and Smithers (1990).

Discussion

The distinction between altricial and precocial young has been applied to many bird and mammal species. Precocial mammals are fully furred, have their eyes open, and are fully mobile shortly after birth. By contrast, altricial young are naked, blind, helpless, and unable to maintain their body temperature. Of the species included in the present study, *E. edwardii* is clearly precocial, while *T. afra* bears altricial young. *A. subspinosus* neonates fall between the two extremes, and are classified here as semi-precocial.

Differences in the mass of individual neonates at birth are related to the length of the gestation period in precocial and altricial species (Neal 1990). The gestation period for the species reported here is not precisely known; however, all pregnant *T. afra* gave birth within 18 days of capture, while *A. subspinosus* and *E. edwardii* produced young at intervals up to 30 days from capture. This corresponds with observations of a short gestation period for *T. brantsii* (22 days) and *T. leucogaster* (28 days) (Scott 1979), longer gestation period (45 days) in *A. dimidiatus* (Al-Khalili and Delany 1986), and a gestation period longer than 50 days in *E. rufescens* (Neal 1982; Rathbun et al. 1981), *E. intufi* (Tripp 1972) and *Macroscelides proboscideus* (Rathbun 1979). Litter sizes were smaller for the semi-precocial *A. subspinosus* and precocial *E. edwardii* than for the altricial *T. afra*, and individual mass and litter mass relative to adult mass were more than two times greater in the semi-precocial and precocial species than in *T. afra*. These results agree with the general trends for precocial and altricial species of African rodents (Neal 1990).

Neal (1990) reported that postnatal growth rates of altricial and precocial rodent species were positively correlated with birth mass, i.e. larger neonates grew faster than smaller neonates. This was the case in the present study, in which young of the larger rodent neonate, *T. afra*, grew at a faster rate than the smaller rodent neonate, *A. subspinosus. E. edwardii* young had a faster growth rate in mass than *A. subspinosus*, but the hindfeet of *E. edwardii* grew more slowly than either of the rodent species.

The present study describes postnatal development in three small mammal species which inhabit the same macro-environment, but employ different reproductive strategies. A fourth species, *Aethomys namaquensis,* occurs in the same habitat, and bears small altricial young which nipple-cling for the first 2–3 weeks of life (Neal 1990). The synchrony of reproduction in the four species trapped in the area was remarkable; 15 of the 16 females trapped were pregnant. Environmental differences and differences in body mass cannot explain the range of reproductive strategies exhibited by these species.

Reference to postnatal development of other *Tatera* species, *Acomys* species, *Elephantulus* species, and *Aethomys* species reveals that many of the patterns observed in this study are shared by other species of each genus. Reproductive parameters are summarized in Table 3. Three southern African *Tatera* species, *T. afra*, *T. brantsii* and *T. leucogaster* have a short gestation period, altricial young, low birth mass relative to adult mass, litter mass approximately 17 % of adult mass, and hindfoot length 21–25 % of adult size (Scott 1979). *T. brantsii* is a partial nipple-clinger, while *T. leucogaster* does not nipple-cling (Scott 1979; Neal 1990). Age at eye-opening is approximately 20 days in all three species. Mean litter size is 2.95 for *T. brantsii,* 3.22 for *T. leucogaster* (Scott 1979) and 4.0 for *T. afra*. Postnatal growth rate in mass is 1 g/day for *T. leucogaster* and *T. brantsii.*

Three *Acomys* species are non-nipple-clingers, with gestation periods longer than 4 weeks (Neal 1983; Al-Khalili and Delany 1986). Individual neonates weigh 13–18 % of adult mass, and litter mass is 31–47 % of adult mass. *A. dimidiatus* (Al-Khalili and Delany 1986) and *A. wilsoni* (Hubbard 1972) neonates are fully furred and have their eyes open at birth, while *A. subspinosus* and *A. hystrella* (Hubbard 1972) develop these characters a few days after birth. Litter size of 1–3 neonates is characteristic of four *Acomys* species for which information is available (Neal 1990), and postnatal growth rates in two species are lower than growth rates of *Tatera* species (Al-Khalili and Delany 1986).

Three *Aethomys* species are nipple-clingers, bearing small altricial young in litters of 3–4 young. Birth mass is 3–6 % of adult mass in all 3 species, and litter mass 13–25 % of adult mass. Eyes open at 8–14 days of age, and incisors are present at birth in all three species. Growth rates vary from 0.45 g/day for *A. namaquensis* (Neal 1990) to 1.6 g/day for *A. kaiseri* (Cheeseman 1981).

E. edwardii, E. rufescens (Neal 1982; Rathbun et al. 1981) and *E. intufi* (Trip 1972) bear litters of 1–2 precocial neonates which do not nipple-cling. Litters of 1–4 young, with a mean litter size of 2.2, have been recorded for *E. rozeti* (Séguignes 1989). Litter mass varies from 28 % of adult mass in *E. rufescens* (Neal 1982) to 42.5 % of adult mass in *E. edwardii*. Gestation periods of 51 days for *E. intufi,* 57 days for *E. rufescens* and at least 75 days for *E. rozeti* have been recorded (Tripp 1972; Rathbun et al. 1981; Séguignes 1989). Growth rate in mass varied from 0.59 g/day for *E. edwardii* to 1.0 g/day in *E. intufi* (Tripp 1972).

Figure 3 presents the results of weighted pair-group cluster analysis of 11 species, based on eight developmental characters. Characters were selected on the basis of availability of information in the literature and included litter size, litter mass relative to adult mass, gestation period, age at eye opening, age at incisor emergence, age at appearance of fur, nipple-clinging, growth rate in mass. The resulting dendrogram clearly demonstrates the grouping of congenerics in clusters, with the exception of one species of *Acomys*. The differences among species, while not clearly related to habitat or body mass, clearly represent the distinction between altricial, semi-precocial and precocial species.

Table 3. **Some life-history parameters for *Tatera afra, T. brantsii, T. leucogaster, Acomys subspinosus, A. dimidiatus, Aethomys chrysophilus, A. namaquensis, A. kaiseri* and *Elephantulus edwardii, E. rufescens, E. intufi***

		Tatera		*Acomys*			*Aethomys*			*Elephantulus*	
	afra[1]	*bra*[2,3]	*leuc*[2]	*subs*[1]	*dim*[4]	*chry*[5,6]	*nam*[6]	*kais*[7]	*edw*[1]	*ruf*[8,9]	*int*[10]
Litter size	4.0	3.0	3.2	3.0	2.4	3.1	3.4	2.6	1.8	1.4	1.6
Litter mass % Adult mass	17.3	17.1	17.2	46.5	31.5	17.7	19.3	13.4	42.5	28.2	32.4
Individ. mass % Adult mass	4.3	5.8	5.3	15.5	13.0	5.7	5.7	5.2	23.6	20.1	20.2
Gestation	–	22	28	–	44	26	–	27	–	57	51
Eyes open	20	17.5	16	9.5	0	12.5	12	9	0	0	0
Incisors erupt	10	6	5.5	7	2.5	0	0	0	0	0	0
Fur visible	7	4	3.5	1	0	0	0	1	0	0	0
Nipple cling[a]	1	1	0	0	0	2	2	2	0	0	0
Growth rate (g/day)	0.82	1.10	0.90	0.55	0.65	0.90	0.45	1.60	0.59	0.77	1.00
Adult mass	95.0[11]	79.9[11]	69.8[11]	21.3[11]	45.0[4]	72.3[11]	46.1[12]	118.0[7]	50.4[11]	52.0[9]	49.2[11]
n	15	130	696	26	359	675	58	?	16	21	19

1 = this study, 2 = Scott (1979), 3 = Measroch (1953), 4 = Al Khalili and Delany (1986), 5 = Brooks (1972), 6 = Neal (1990), 7 = Cheeseman (1981), 8 = Neal (1982), 9 = Rathbun et al. (1981), 10 = Tripp (1972), 11 = Skinner and Smithers (1990), 12 = De Graaff (1981).
[a] 0 = no nipple-clinging, 1 = nipple-clinging 1–4 days after birth, 2 = nipple-clinging from birth.

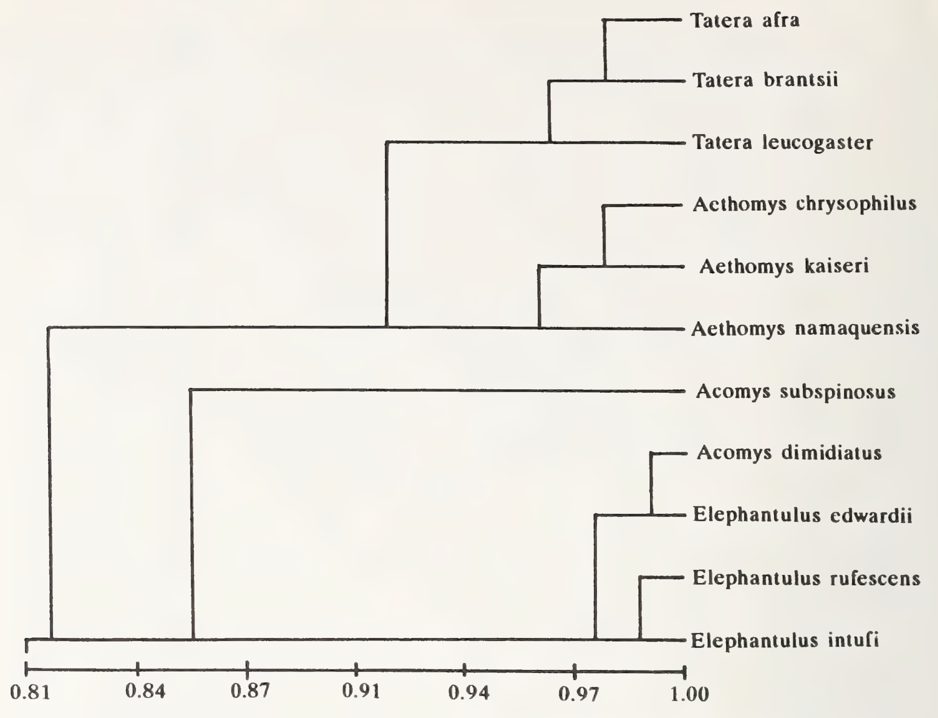


Fig. 3. Dendrogram derived from weighted-pair group cluster analysis based on a correlation matrix of eight developmental characters (listed in text). Values along x-axis are similarities

With the accumulation of information on neonatal development of several species belonging to the same genus, it is apparent that the level of development of young at birth is fixed with a genus. Thus three *Tatera* species, four *Gerbillurus* species (DEMPSTER and PERRIN 1989; DEMPSTER and PERRIN 1991), three *Mus* species (NEAL 1990) all have altricial young. Three *Otomys* species and three *Acomys* species have precocial young (NEAL 1990), with *A. subspinosus* and *A. hystrella* (HUBBARD 1972) bearing semi-precocial young. All elephant-shrew species are reported to bear precocial young (RATHBUN 1979). The designation of "semi-precociality" is unclear: NEAL (1990) classifies *Aethomys* species as altricial despite the fact that all developmental events such as eye opening, incisor eruption, and hair growth occur earlier than in *Tatera* species. Clearly the altricial-precocial distinction represents a continuum, with species exhibiting different levels of altricial or precocial development.

This study has clearly shown that the most important factor influencing the developmental strategies of the species included here is altricial/precocial development, which is a phylogenetically conservative character in small mammals.

Zusammenfassung

Postnatale Entwicklung bei drei sympatrischen Kleinsäugerarten aus Südafrika

Vier Arten kleiner Säuger kommen gemeinsam in einer trockenen Region der südwestlichen Kapprovinz vor. Mehrere Weibchen aller dieser Arten warfen Junge, nachdem sie während einer Feldexkursion im September 1990 gefangen worden waren. Erstmalig wird hier über die Frühentwicklung der drei Arten, *Tatera afra, Acomys subspinosus* und *Elephantulus edwardii* berichtet. Die erhobenen Daten werden ferner mit entsprechenden Ergebnissen der vierten Art, *Aethomys namaquensis,* verglichen.

T. afra brachte pflegebedürftige, an der Brustwarze haftende Junge zur Welt, während die Jungen von *E. edwardii* frühreif waren und nicht an der Brustwarze hafteten. *A. subspinosus* brachte Junge in einem Zwischenstadium hervor, die aber sehr schnell wuchsen. Die Jungtiere von *A. namaquensis* gelten zwar als pflegebedürftig, aber ihr Entwicklungsstadium bei der Geburt ist weiter fortgeschritten als bei *T. afra*.

Verschiedene Habitate und Körpergrößen können diese Unterschiede nicht erklären. Andere Arten der untersuchten Gattungen zeigen ähnliche Entwicklungsabläufe, mit Ausnahme der *Acomys*-Arten. Nesthocker- und Nestflüchter-Ontogenesen werden daher als phylogenetisch konservative Merkmale bei diesen Kleinsäugern bewertet.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Bats from Mana Pools National Park in Zimbabwe and the first record of *Eptesicus rendallii* from the country

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The bat fauna of Africa is not well documented compared to other African mammals. For example, while the bats of Zimbabwe have received some attention (Fenton 1975; Smithers and Wilson 1979; Hutton 1986), at most locations there has been no specific survey of bats. Even at Mana Pools National Park on the Zambezi River (15° 44′ S; 29° 21′ E), the site of some bat research (e.g. Aldridge et al. 1990; Fenton et al. 1990; Obrist et al. 1989), there is virtually no information about the bat fauna.

Between 18:00 and 21:00 we used 12 m mist nets (126 net hours in November 1987) and two macro-mist nets (36 net hours in June 1990; Rautenbach 1985) to sample bats at sites within 10 km of the headquarters of Mana Pools National Park. We sampled sites in the dry woodland some distance away from the river, and on the flood plain of the Zambezi River in the predominately *Acacia albida* woodland along the Zambezi River, a park-like habitat with dispersed tall canopy trees and little understory (Dunham 1989). Here we record the first record of *Eptesicus rendallii* from Zimbabwe and the occurrence of 20 species of bats in Mana Pools National Park (Table 1), 15 of which are recorded for the first time.

The bats recorded for Mana Pools National Park are compared with the species compositions of two other sites in southern Africa (Table 1). These bat faunas are typical of open woodland in southern Africa. *Nycticeius schlieffenii* and *Scotophilus borbonicus* together accounted for 80 % of the 136 bats netted at Mana Pools National Park between 18:00 and 21:00 over 12 nights in June 1990. In comparing the faunas (see Table), it is clear that a number of species are rarely encountered, while others are taken only in the immediate vicinity of their roosts. The larger species richness recorded for Pafuri, may be ascribed to greater ecological complexity and more intensive surveying.

Eptesicus rendallii is widespread in open woodland savannahs of subsaharan Africa (Smithers 1983) and ranges southwards into northern Botswana (Smithers 1971), central Zambia (Ansell 1978), southern Malawi (Ansell and Dowsett 1988), and the Tete and Mocambique districts of Mocambique (Smithers and Lobao Tello 1976). Our specimens are the first from Zimbabwe and they have been prepared as standard skin and skull vouchers and deposited in the national mammal collection of the Transvaal Museum. In wing characteristics (aspect ratio 6.71 male, 6.18 female; wingloading 7.81 N m^{-2} and 6.93 N m^{-2}) and size (6.0 and 6.5 g) these bats would be included in the Group 1 of Aldridge and Rautenbach (1987), species with high flight manoeuvrebility that should forage in relatively cluttered situations.

We prepared standard bone marrow karyotypes from the two *E. rendallii* using the in vivo technique of Robbins and Baker (1978) as modified by Baker et al. (1982). At least

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The bats captured at Mana Pools National Park compared with species recorded in the Sengwa Wildlife Area in Zimbabwe (18° 10′ S; 28° 13′ E) and the Pafuri area of the Kruger National Park in South Africa (22° 25′ S; 31° 13′ E)

While the actual numbers of bats from Mana Pools National Park are shown, for the other two sites relative abundance (for comparable sampling effort) is indicated as follows: * <3; + = 3–10; ++ = 11–20; +++ = 21–30; ++++ = 31–40, etc. The "r" identifies bats captured emerging from roost sites, not in nets set in woodland. The "a" is from SMITHERS and WILSON (1979); the "b" from FENTON et al. (1990); the "c" from ALDRIDGE et al. (1990); the "d" from HUTTON (1986); and the "e" an observation of THOMAS VOLPERS (pers. comm.)

Species	Mana Pools	Sengwa	Pafuri
Epomophorus wahlbergi	–	+	+
Epomophorus crypturus	1	++	*
Rousettus aegyptiacus	–	+	++
Taphozous mauritianus	+[a]	*	*
Nycteris grandis	+[b]	–	–
Nycteris woodii	–	+	*
Nycteris thebaica	+[c]	++	+
Rhinolophus hildebrandtii	1	+	+
Rhinolophus fumigatus	–	+	+
Rhinolophus clivosus	–	*	*
Rhinolophus darlingi	1	–	*
Rhinolophus landeri	*[d]	+[r]	*
Rhinolophus simulator	–	+[r]	*
Rhinolophus swinnyi	–	–	*
Hipposideros commersoni	1[e]	+	*
Hipposideros caffer	–	+++[r]	+++[r]
Cloeotis percivali	–	*[r]	–
Miniopterus schreibersii	1	+	*
Myotis welwitschii	–	*	*
Myotis tricolor	–	–	*
Myotis bocagei	–	–	*
Pipistrellus rueppellii	1	++	+
Pipistrellus rusticus	–	–	+++
Pipistrellus nanus	1	++	+
Chalinolobus variegatus	6	*	*
Laephotis botswanae	–	+	*
Eptesicus rendallii	2	–	–
Eptesicus hottentotus	–	–	*
Eptesicus cf. *melckorum*	3	?	+
Eptesicus zuluensis	1	*	+
Eptesicus capensis	4	+++	++
Scotophilus dinganii	–	+	++++
Scotophilus borbonicus	52	++++	++++
Nycticeius schlieffenii	55	++++	++++
Kerivoula argentata	–	*	*
Kerivoula lanosa	–	–	*
Otomops martiensseni	–	*	–
Tadarida fulminans	–	*	*
Tadarida bivittata	–	+	–
Tadarida ansorgei	–	–	*
Tadarida nigeriae	–	+	–
Tadarida chapini	–	++	–
Tadarida pumila	7	–	++[r]
Tadarida midas	1	–	+[r]
Tadarida condylura	–	–	++[r]

five representative chromosome spreads were examined from each bat to determine diploid (2n) and fundamental numbers (FN). Photomicrographic enlargements of suitable spreads were used in the final analyses and to prepare a karyogram.

Our data show that the standard karyotype of *E. rendallii* is 2n = 38, FN = 50, and the autosomal complement is seven pairs of bi-armed chromosomes, and a size-graded series of 11 acrocentric pairs. A prominent secondary constriction is apparent near the centromere of one of the larger pairs of acrocentric chromosomes. The X chromosome is a large, submetacentric, and the Y a small submetacentric. Our findings agree with the earlier description of the karyotype of *E. rendallii* (McBee et al. 1987), with the exception of the Y chromosome, which is described for the first time.

Some workers (e.g. Heller and Volleth 1984) would group *E. rendallii* together with other karyotypically variable *Eptesicus*-like African bats, as *Pipistrellus* since they deviate from what is considered to be the typically conservative karyotype of 'true' *Eptesicus* (2n = 50). Based on bacular morphology others (e.g., Hill and Harrison 1987) also consider *E. rendallii* as a *Pipistrellus*. However, the complexity of the problem makes it prudent to report our record as *Eptesicus rendallii,* pending the results of more in-depth systematic studies.

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Further notes on the pupping period in a recently founded colony of Grey Seals *(Halichoerus grypus)* in the Netherlands

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In a short paper published previously ('T HART et al. 1988), we reported on the birth of Grey Seals, *Halichoerus grypus* (Fabricius, 1791), living on and near a high lying shoal off the Frisian Island of Terschelling, the Netherlands. In that recently founded colony, consisting of only young animals, in the second week of January 1985, the first two just-born Grey Seals were observed. The next two years, two very young specimens were seen during the last week of January, three newly born Grey Seals during the first week of February and 10 days later again two just-born pups were observed. Then we drew attention to the fact that the founders of the colony in the Netherlands almost certainly came from the Farne Islands, where the pupping period is from mid October till mid December with a peak around November 7th.

We believed it interesting to follow the development of the Dutch colony of Grey Seals, in particular the changes in the reproduction period. Thanks to the observations of the pilots of the Air Force base at Leeuwarden, and the staff of the lighthouse "De Brandaris" on the island, we could gather a number of data, supplemented by data on very young animals found beached after heavy storms on nearby lying islands and on the coast of the continent (Table).

Births of Grey Seals in the Netherlands per decade, season 1987/88 to 1990/91

To these births must be added a newly-born male found late October/early November 1990

		December			January			February
1987/1988					xx	xxx		
1988/1989				xx	x	xx		x
1989/1990				xx	xx	x	x	
1990/1991		x	x	xxxxx	x	x		

The data compiled in the table show clearly a shift of the pupping period to an earlier date in the season. This shift confirms the observations by BACKHOUSE and HEWER (1957) that primiparous Grey Seals give birth later in the season than females which had already one or more pups. We wonder whether the trend to reproduce at an earlier date will continue till there will be a similar period of pupping in the Netherlands as in the Farne Islands colony, or than the more southern situated colony in the Netherlands will have its own reproduction period.

We like to thank sincerely all the persons who helped us in obtaining the data, in particular messrs. HESSEL WIEGMAN, OTTO OVERDIJK and the staff of the lighthouse "De Brandaris".

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Lack of biochemical-genetic variation in native Sika deer (*Cervus nippon hortulorum*) from the far east of the Asian continent

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In contrast to various other deer species (see Hartl et al. 1990, for review), Sika deer (*Cervus nippon*) has only poorly been investigated for biochemical-genetic variation. Population genetic data are available only from representatives of the Japanese subspecies *Cervus nippon nippon,* introduced into Great Britain and Ireland, and from hybrids of this subspecies with the Red deer (*Cervus elaphus scoticus;* see Harrington 1973). A multilocus investigation including 11 RBC/plasma enzyme systems was performed by Herzog (1988) without detecting polymorphism or differences from the Red deer except for 6-phosphogluconate dehydrogenase, where the occurrence of genetic polymorphism is indicative for hybrid populations of Red and Sika deer.

In order to examine genetic variation in native Sika deer from the easternmost point of Asia, possibly belonging to the subspecies *C. n. hortulorum* (Ratcliffe 1987), whole blood samples of 43 individuals from a population in Primor'e (USSR) were collected during the hunting season of 1989/1990. The blood was fractioned into plasma and erythrocytes and stored frozen at −20 °C. Horizontal starch gel and agarose gel electrophoresis, blood protein and enzyme staining as well as the interpretation of band-patterns were done as summarized by Hartl and Höger (1986), Hartl et al. (1986) and Hartl and Ferrand (1991). The following blood proteins and enzymes were screened (abbreviation, E.C. number and gene loci scored are given in parentheses): hemoglobin (Hb, alpha and beta chain, *Hb-α, Hb-β*), transferrin (Tf, *Tf*), lactate dehydrogenase (LDH, E.C. 1.1.1.27, *Ldh-2*), NADH-diaphorase (DIA, E.C. 1.6.2.2, *Dia*), catalase (CAT, E.C. 1.11.1.6, *Cat*), aminoacylase-1 (ACY-1, E.C. 3.5.1.14, *Acy-1*), and glucose phosphate isomerase (GPI, E.C. 5.3.1.9, *Gpi-1*).

None of the gene loci investigated was polymorphic in the Sika deer. When compared to band-patterns in the Red deer (*C. e. hippelaphus*), allelic differences were observed at the *Hb-β* and the *Cat* locus. Whereas the lack of genetic variation in introduced Sika deer (*C. n. nippon;* Herzog 1988) can be explained by genetic drift and inbreeding, which are frequently associated with the artificial foundation of populations (comp. Hartl et al. 1986; Hartl 1989), this result was not to be expected in our native Sika deer population. As far as the evolutionary rate of proteins is concerned, some of the blood proteins and enzymes investigated showed considerable genetic variation in other deer species (see Hartl et al. 1990, and references therein). Further studies are required to elucidate the population history and distribution of Sika deer in our study area as well as its genetic structure to detect a possible threatening by genetic pauperization. Concerning the genetic differences from the Red deer, the fixation of alternative alleles at two out of eight loci is in accordance with allozyme differentiation at the species level.

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A comparison of genetic diversity in Nubian ibex (*Capra ibex nubiana*) and Alpine ibex (*Capra i. ibex*)

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Alpine ibex (*Capra i. ibex*) have shown a remarkable recovery in recent decades after almost becoming extinct in the last century (Grodinsky and Stüwe 1987). The recovery was the result of an alpine-wide, though largely uncoordinated conservation effort, re-establishing ibex populations through reintroductions and translocations (Stüwe and Nievergelt 1991). Despite the dramatic increase in ibex population numbers and often strong population growth, little attention has been given to the relationships of reintroduction methodology (i. e. number of founders, sex ratio, and number of releases) and population genetic characteristics.

Maintenance of heterozygosity levels or minimization of loss of genetic variability has become a primary goal in the population management of vulnerable species (Lande and Barrowclough 1987). Recent population surveys have shown that genetic variability in alpine ibex was low when compared to that in natural populations of other ungulate species (Stüwe and Scribner 1989; Randi et al. 1991). Genetic similarity among ibex populations was related to stocking history, probably as a result of genetic drift occurring during reestablishment of the populations (Stüwe et al. 1991). A detailed analysis of the effects of such management actions on the genetic diversity of the newly founded populations may aid the development of strategies for future reintroductions of locally extinct populations of ibex and other species. To determine whether low alpine ibex genetic diversity was a result of management actions or was a phenomenon reflecting species-wide evolutionary history, we compared alpine ibex with Nubian ibex (*Capra ibex nubiana*), using the same genetic methodology. The latter were chosen as a control because no unmanaged alpine ibex populations exist, and the Nubian ibex appears to be the taxa geographically and systematically closest related to alpine ibex. We chose a population in the Negev desert currently numbering about 400 individuals (Alkon and Man 1988). Several Nubian ibex populations have suffered severe population reductions in the past (Baharav and Meiboom 1981; Krausman and Shaw 1986; Habibi and Grainger 1990). However, there is no evidence that the Negev population has undergone the repetitive reductions in population size, and the intensive management actions alpine ibex experienced in recent times.

Blood was analyzed from 149 alpine ibex captured 1988 through 1990 in the four French populations Bargy (n = 22), Champagny (n = 10), Encombre (n = 14), and Maurienne (n = 37), the three Swiss populations Saastal (n = 29), Jollital (n = 5), and Mont Pleureur (n = 11), and the Italian population Gran Paradiso (n = 21). An additional 39 blood samples were obtained from Nubian ibex, caught in 1988 in Avdat Canyon National Park and Zin Nature Reserve, near Sede Boqer, Israel. Blood samples were obtained from live animals immobilized with Xylazine-based tranquilizing drugs (Stüwe and Scribner 1989).

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Fourteen enzymes encoded at 15 loci were examined for polymorphisms using horizontal starch-gel electrophoresis (Manlove et al. 1976): albumin (ALB), phosphoglucomutase-3 (PGM-3; EC 2.7.5.1), hemoglobin (HB), glucose phosphate isomerase-1 (GPI-1; EC 5.3.1.9), creatine kinase-2 (CK-2; EC 2.7.3.3), glucose-6-phosphate (G-6-P; EC 1.1.1.49), malate dehydrogenase-1 (MDH-1; EC 1.1.1.37), 6-phosphogluconate dehydrogenase (PGD; EC 1.1.1.44), malic enzyme-1 (MOD-1; EC 1.1.1.40), purine nucleoside phosphorylase (NP; EC 1.6.2.2), lactate dehydrogenase-1 (LDH-1; EC 1.1.1.2), eurythacytic acid phosphatase (EAP), peptidase-B (PEP-B; leucyl glycyl glycine as substrate; EC 3.4.11) and indophenol oxidase-1,2 (IPO-1,2; EC 1.15.1.1). Initial sample treatment and analysis followed Stüwe and Scribner (1989).

Differences in levels of multi-locus heterozygosity were tested using contingency chi-square analysis (Sokal and Rohlf 1981).

The percentage of polymorphic loci (13.3 % and 20.0 %), mean number of alleles per locus (1.2 and 1.5), and average direct-count heterozygosity (0.048 and 0.087) were all lower in alpine than in Nubian ibex, respectively (Table). Differences in multi-locus heterozygosity were significant ($\chi^2 = 24.64$, $P < 0.001$, $df = 3$).

Direct-count estimates of average heterozygosity, mean number of alleles per locus, percent of polymorphic loci, and allele frequencies at seven variable loci in alpine and Nubian ibex

Locus	Alpine ibex	Nubian ibex	Locus	Alpine ibex	Nubian ibex	Locus	Alpine ibex	Nubian ibex
NP 118	0.000	0.026	MDH-2 70	0.000	0.013	PGD 90	0.003	0.205
NP 100	1.000	0.949	MDH-2 100	1.000	0.987	PGD 100	0.997	0.795
NP 82	0.000	0.026	LDH-1 88	0.510	1.000	Sample size	149	39
MOD-1 100	1.000	0.231	LDH-1 100	0.490	0.000	Avg. H	0.048	0.087
MOD-1 111	0.000	0.769	PEP-B 100	0.678	0.000	# of alleles	1.2	1.5
EAP 86	0.000	0.026	PEP-B 112	0.322	0.769	% polym.loci	13.3	20.0
EAP 100	1.000	0.974	PEP-B 136	0.000	0.231			

Locus designations are provided in the text.

Average Rogers (1972) genetic distance between Nubian and alpine ibex was 0.106, far exceeding the genetic distance among alpine populations (mean: 0.021, range: 0.002–0.058). However, this relationship is based on few loci, and is primarily due to the presence of unique alleles and frequency differences. Allelic variation among the 149 alpine ibex was detected at three loci out of 15 loci analyzed; PGD, LDH-1 and PEB-B. Among 39 Nubian ibex, six loci were variable: NP, MOD-1, EAP, MDH-2, PEB-B, and PGD. Of the seven loci variable among both taxa, only one locus (LDH-1) was fixed in Nubian ibex as compared to four loci (NP, MOD-1, EAP, and MDH-2) fixed in alpine ibex (Table 1). In addition, the PGD 90 allele was present in only one individual in alpine ibex (frequency: 0.003) but was found at a much higher frequency in Nubian ibex (0.205), indicating progressing fixation among alpine ibex. The PEB-B 112 allele was found in both taxa, while the PEB-B 100 allele was found in alpine ibex and the PEB-B 136 allele was found in Nubian ibex only (Table).

Alpine and Nubian ibex are not sympatric and there are no fossil indications they ever were since the radiation of *Capra* in the third faunal zone of the Pleistocene. Their taxonomic status is controversial. Both are considered subspecies by many authors (see Schaller 1977 for review), although Heptner (1966), and Hartl et al. (1990) separate them as species. Hartl et al. (1990) calculated the genetic distance by biochemical comparison of one individual each of alpine ibex, Nubian ibex, markhor (*Capra falconeri*), and Bezoar goat. Of these four taxa only alpine and Nubian ibex had previously been

considered subspecies (SCHALLER 1977). However, HARTL et al. (1990) found the greatest genetic distance between just those two, and suggested that these taxa also be considered separate species.

Since the separation of alpine and Nubian ibex from their common ancestor, allelic variation could either have been lost (through drift or selection), or added (through mutation). This could have occurred either as a natural consequence of intrinsic population processes, or as a result of manipulative processes in either of the taxa. We believe genetic divergence between alpine and Nubian ibex should not be based solely on time since common ancestry as used in genetic distance calculations. Such calculations assume on homogeneity of evolutionary rates within independent lineages. However, the severe population manipulations experienced by alpine ibex since the 16th century (STÜWE and NIEVERGELT 1991) very likely contributed to the shifts in allele frequencies, the loss of alleles, and the significantly lower level of heterozygosity observed today. The low genetic diversity discussed for Alpine ibex populations (HARTL 1986; STÜWE and SCRIBNER 1989; RANDI et al. 1991) as well as the observed genetic distance between alpine and Nubian ibex may thus be due in part to stochastic effects associated with human intervention rather than deterministic processes alone.

It is difficult to assess the significance of the degree of genetic divergence between Nubian and Alpine ibex in the absence of molecular markers which exhibit alternative fixation, and in light of the strong influence of human manipulations. Without further genetic comparisons within the genus *Capra* our results do not warrant a classification of alpine ibex and Nubian ibex as separate species, and we therefore accept the systematic evaluation by SCHALLER (1977).

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BUCHBESPRECHUNGEN

WEHNER, R.; GEHRING, W.: **Zoologie.** 22., völlig neu bearbeitete Auflage. Stuttgart, New York: Georg Thieme 1990. 816 S., 406 Abb., 30 Tab. DM 48,–. ISBN 3-13-367422-6

Dies ist eine Neuauflage des 1922–1969 in 17 Auflagen erschienenen „Grundriß der allgemeinen Zoologie" von ALFRED KÜHN, der in 18.–21. Auflage unter dem Titel „Allgemeine Zoologie" von E. HADORN und R. WEHNER fortgesetzt wurde. Die letzte gründlich umgearbeitete Fassung aus dem Jahr 1974 ist inzwischen veraltet. Das nun vorliegende Buch wurde zwar in der Grobgliederung mäßig, in Stoff und Abbildungen aber stark verändert. Unter den Abbildungen sind viele zweifarbig, außerdem gibt es als Neuheit eine Reihe von Licht-, TEM- und REM-Fotos. Der Umfang ist gegenüber der letzten Auflage erheblich erweitert. Die Kapitel über Zytologie, Vererbung und Entwicklung stammen von W. GEHRING, die übrigen von R. WEHNER. Die beiden Autoren hatten also die schwierige Aufgabe, große Bereiche der Zoologie überblicken und kompetent darstellen zu müssen. Der Vorteil ist eine einheitliche und geschlossene Behandlung des Stoffes mit konsequent befolgten Definitionen und Begriffen und zahlreichen Querverweisen. Auch die Versuchung, Teilgebiete zu bevorzugen und andere zu vernachlässigen, ist dadurch eingeschränkt. Erfreulich ist das Bemühen, die experimentellen Belege und die Geschichte grundlegender Anschauungen wie in der Zytologie und Vererbung zu skizzieren, damit das Verständnis zu erleichtern und den Text aufzulockern. Ob die moderne Genetik so ausführlich noch in eine „Zoologie" hineingehört, wäre zu überlegen, ungeachtet der Tatsache, daß sich die vorliegende Darstellung wirklich spannend liest. Die Autoren werden allerdings auch den Intentionen des Begründers ALFRED KÜHN insofern gerecht, als dieser stark genetisch orientiert war.

Bei der Beurteilung eines solchen Buches fragt man: Wurde die Zoologie vollständig und ausgewogen abgehandelt? Ist alles Wichtige enthalten, wurde nichts vergessen? Sind die mitgeteilten Fakten notwendig und ausreichend? Was wurde aufgegeben, was neu aufgenommen? Ist das Aufgegebene tatsächlich überflüssig, das neu Aufgenommene hinreichend gesichert? Bildet das Buch heute noch eine gute Wissensgrundlage und einen Überblick über das Fach?

In der Einleitung weisen die Autoren darauf hin, daß in der Molekular- und Zellbiologie wie auch in Ethologie, Ökologie und Evolutionsbiologie besonders große Fortschritte zu verzeichnen seien. Diese Kapitel sind in der Tat am stärksten verändert. Proteinsynthese, Zellkontakte, Immunologie, hüpfende Gene, Rotroviren, der Zellstammbaum des Nematoden *Caenorhabditis,* homoetische Mutationen bei *Drosophila*, molekulare Mechanismen der Hormonwirkung, die Zugorientierung der Vögel, die Soziobiologie und der Kladismus sind nur einige Stichworte. Neue Erkenntnisse klären ehemals offene Fragen, korrigieren falsche Vorstellungen und ermöglichen es bisweilen, bekannte Tatsachen unter übergeordneten Gesichtspunkten zusammenzufassen. Insofern müssen sie nicht unbedingt zu einer Stoffvermehrung führen. In anderen Fällen allerdings verleiten sie dazu, wichtige, jedoch schon länger unumstrittene Grundlagen zurückzustellen zugunsten erst später geklärter Folgefragen. Für den Anfänger ergeben sich daraus Lücken, die er auf andere Weise schließen muß, die ihm aber das Verständnis erschweren. So erscheinen aus heutiger Sicht Abschnitte aus der 19. Auflage wie „die Zelle im Gewebeverband" oder das dihybride Kreuzungsschema für Rinder, die Genwirkkette des Phenylalanins bei *Drosophila* oder auch das Schema für das Zustandekommen des Kniesehnenreflexes vielleicht antiquiert. Ihr Fortfall macht die Zoologie aber wieder ein Stück abstrakter. Ein Teil der alten Abbildungen wurde in verkleinerter Form wiedergegeben wie der Gewebeschnitt eines Schwammkörpers, in dem nun noch weniger von den Choanozyten zu erkennen ist als früher. Ausgeglichen wird dieser Nachteil durch meist prägnantere Zeichnungen. Diese sind fast stets gründlich beschriftet und erklärt und sind auch meist notwendig. Aber auch alte, scheinbar unproblematische Darstellungen sollten gründlicher überdacht werden. So werden in Abb. 12.92 Selachier- und Teleosteer-Herz verglichen. Der wohl auffallendste Unterschied – reduzierter Bulbus cordis, dafür Bulbus arteriosus bei Teleosteern, kommt nicht zum Ausdruck. Dafür fehlen die bei den Selachiern nicht eingezeichneten Sinu-Atrialklappen dort in Wahrheit nicht, und was im Knochenfisch-Schema als „Perikard" bezeichnet wird, kommt dort in Wahrheit nicht vor.

Der Schultergürtel eines Vogels (Abb. 12.86) ist in folgenden Punkten weniger richtig als in der älteren Auflage: Humerus gelenkt nicht allein am Coracoid, sondern auch an der Scapula: Furcula-Spitze ist mit Sternum-Spitze meist sehnig verbunden, liegt jedenfalls nicht darüber; Coracoid setzt seitlich am Sternum und nicht ventral an. Beim Säugerhaar sitzt der Musculus arrector pili auf der falschen Seite. Der Schnitt durch die Amphibienhaut gibt die Umrisse der Drüsenepithelzellen in Schleim- und Körnerdrüse falsch wieder. Bei Pferd und Mammut zeigen Pfeile zu den Kauflächen der Molaren nicht auf Zement-, sondern Dentinflächen.

Wie bei den Abbildungen, so auch beim Inhalt: Unter einer Vielzahl folgerichtiger, genauer, gut verständlicher und einprägsamer, richtiger Darstellungen stößt man gelegentlich auf Fehler. Die Sehnervenfasern werden auch bei den Säugern im Zwischenhirn verschaltet (s. 371), der Frosch hat keinen Neocortex (S. 372), Amygdala ist keine Rindenstruktur (S. 373). Bildweite ist nicht gleich Brennweite (Abb. 7.14 C), auch die Neunaugen haben in Ruhe nahakkomodierte Augen (S. 413). *Talpa* und Scalopus dürften entgegen S. 516 auf einen gemeinsamen, bereits grabenden Vorfahr

zurückgehen. Das Fehlen eines Brustbeins bei *Archaeopteryx* kann man nicht gut als Reptilienmerkmal ansehen, wenn fast alle Reptilien ein Sternum besitzen (S. 553). Auf den Galapagos-Inseln gab es vor Ankunft des Menschen nicht bloß zwei, sondern etwa 9 terrestrische Säugerarten (s. S. 562). Beim biologischen Artbegriff (S. 576/577) spielt immer noch eine „Morphospezies-Definition" eine verwirrende Rolle. Es kann nicht für ein einheitliches Phänomen zwei nicht deckungsgleiche Definitionen geben. Die Morphologie liefert Kriterien, mit deren Hilfe man die Grenzen von Biospezies oft ohne allzu großen Aufwand erkennen kann, aber sie definiert keine Biospezies. Die Amphibien besitzen durchaus einen Sinus venosus (s. 735), bei den Säugetieren sitzt das Foramen ovale nicht im Ventrikel, sondern im Interatrialseptum des Herzens. Der Metatarsus 1 der Vögel ist frei und entgegen S. 763 nicht in den Tarsometatarsus einbezogen, dieser enthält dafür auch ein Metatarsale 4. *Hylobittacus* ist keine Skorpionsfliege (S. 482, 483), sondern eine Mückenhaft.

Diese und weitere kleine Fehler verlieren sich glücklicherweise in dem reichhaltigen Inhalt. Die klare Gliederung mit farblich hervorgehobenen „Boxen" und Tabellen wie auch neue Ideen, z. B. die Aufteilung des Verhaltens-Kapitels oder die Einbeziehung der Biolumiziszenz in das Bewegungs-Kapitel sorgen für Abwechslung und zusätzliche Spannung bei der Lektüre des weithin sehr fesselnd dargebotenen Inhalts. Der Verweis auf speziellere Literatur und Übersichtsreferate in den „Verhandlungen der Deutschen zoologischen Gesellschaft" der letzten 15 Jahre regen zu vielseitiger Vertiefung an. Insgesamt eine erstaunliche Arbeitsleistung. Der Inhalt geht sicherlich weit über das hinaus, was ein Student im Grundunterricht noch bewältigen kann. Das Buch ist eigentlich jedem Zoologen zu empfehlen, der in der Explosion des Wissens einen handlichen Überblick sucht.

J. Niethammer, Bonn

Walser, K.; Bostedt, H. (Hrsg.): **Neugeborenen- und Säuglingskunde der Tiere.** Stuttgart: Ferdinand Enke Verlag 1990. 576 pp., 251 Abb., davon 84 farbig auf 32 Farbtaf., 120 Tab. DM 198,–. ISBN 3-432-38381-6

15 Autoren aus Deutschland und je einer aus der Schweiz und den USA haben ein klar gegliedertes und praxisorientiertes Buch verfaßt, welches vom Verlag mit technischer Sorgfalt und optisch sehr ansprechend herausgegeben wurde.

In den einleitenden drei der insgesamt zwölf Kapitel werden folgenden Probleme behandelt: 1. Anatomische und physiologische Grundlagen des Neugeborenen; 2. Das Verhalten der Neugeborenen und Säuglinge; 3. Grundlage der Ernährung von Neugeborenen. Es schließen dann drei Kapitel an, welche für die Aufzucht und Pflege neugeborener Säuger von besonderer Bedeutung sind: 4. Fütterungspraxis; 5. Die Haltungsbedingungen für Jungtiere von der Geburt bis zur Entwöhnung; 6. Pränatale Entwicklungsstörungen.

Die folgenden sechs Kapitel des Buches dürften besonders für den tierärztlichen Praktiker hilfreich sein. Es werden die Krankheiten von Fohlen, Kälbern, Schaf- und Ziegenlämmern, Ferkeln, Hunde- und Katzenwelpen sowie von Neugeborenen und Säuglingen verschiedener Zoo- und Wildsäugetierarten behandelt. Bei den Krankheiten werden Vorkommen und Bedeutung, klinisches Bild, pathologischer Befund, Diagnose und vor allem die Therapie nebst möglichen Komplikationen geschildert.

Vornehmlich zu den praxisorientierten Kapiteln finden sich auf 32 Farbtafeln Darstellungen zu Krankheitsbildern. Dabei ist jede der Farbtafelseiten mit einem kräftigen Farbbalken gekennzeichnet, so daß das Auffinden de Illustrationen erleichtert wird. Ein mehr als zehnseitiges Register erschließt den Inhalt des Bandes.

Ein bedeutender Vorzug des Buches besteht darin, daß viele Einzelabschnitte der Kapitel jeweils durch eine eigene weiterführende Literaturliste abgeschlossen werden. Den Herausgebern und Autoren ist auch dafür Anerkennung zu zollen, daß sie die Herkunftspublikationen der Daten in den sehr reichlich im Text verteilten Tabellen klar nennen. Viele – auch moderne – Lehrbücher erfüllen diese eigentlich selbstverständliche Bedingung leider nicht!

Die Schilderung der normalen und pathologischen Verhältnisse bei Haustieren macht einen großen Anteil des Buches aus. Es wird sicherlich auch von Säugetierkundlern und von Personen, die mit der Pflege von Neugeborenen und Jungtieren befaßt sind, mit Nutzen zu Rate gezogen werden. In diesem Zusammenhange sind die Ratschläge und praktischen Hinweise für die mutterlose Aufzucht von jungen Säugetieren besonders hervorzuheben.

P. Langer, Gießen

Wünnenberg, W.: **Physiologie des Winterschlafes.** Mammalia depicta, Heft 14, Beiheft zur Zeitschrift für Säugetierkunde. Hamburg und Berlin: Paul Parey 1990. 98 S., 34 Abb., 16 Tab. DM 58,–. ISBN 3-490-12118-X

Mit dem Wunsch nach einer Verlängerung des menschlichen Lebens taucht auch heute immer wieder die Frage auf, ob sich das irdische Dasein nicht durch einen „künstlichen" Winterschlaf unterbrechen ließe, um es später wieder „in alter Frische" weiterzuführen. Ganze Forschergenerationen haben versucht, das Geheimnis des „Winterschlafes" zu lüften. Die Zahl der Untersuchungen geht in die

Tausende. Es gibt viele aufregende Entdeckungen; von der Lösung des Rätsels sind wir aber noch weit entfernt. Was ist Winterschlaf? Sicher ist es keine „Pause“ vom Leben. Die vorliegende Publikation gibt eine Reihe grundsätzlicher Antworten. Es war dabei notwendig, die Begriffe „Homoiothermie“ und „Poikilothermie“ neu zu definieren und sie mit der Problematik zu Überwinterung zu versehen. Die wichtigsten Merkmale des natürlichen Winterschlafes (Inaktivität, Stoffwechselreduktion, erniedrigte Körpertemperatur und Erregbarkeit) erlauben heute eine Zuordnung zu dem Phänomen des Torpors. Der Hauptabschnitt beginnt mit den Steuerungsmechanismen (exogene und endogene Faktoren). Sie veranlassen die Vorbereitungen auf den Winterschlaf (Vorratsspeicherung, Anlage von Fettdepots, Aufsuchen oder Herstellen geeigneter Winterquartiere). Nur nach Abschluß dieser Maßnahmen kann ein Winterschlaf auch zum Erfolg führen. Erst jetzt ändert sich die Temperaturkontrolle mit einem kennzeichnenden Wechsel zwischen Torpor- und Euthermiephasen, wobei sich in der Wintermitte nicht nur die tiefsten Körpertemperaturen, sondern auch die längsten Schlafperioden einstellen. Zur Deutung dieser Zyklen werden „Sollwertverstellungen“ bei der Regelung der Körpertemperatur herangezogen. In enger Verbindung damit kommt es zu Minimaleinstellungen in allen wichtigen Organsystemen (Herz, Kreislauf, Atmung, Stoffwechsel, Elektrolyt- und Wasserhaushalt, Nervensystem, endokrines System). In zahlreichen Fällen lassen sich bereits ursächliche Zusammenhänge darstellen, insbesondere die entscheidenden energetisch-ökonomischen Prozesse. Trotz der Fülle an Informationen bleiben die eigentlichen „Auslöser“ des Winterschlafes bis heute im Dunkeln. Auch die Untersuchungen über mögliche „Triggersubstanzen“ haben hier noch keinen Durchbruch erzielt.

Das Beiheft ist in erster Linie für die Studierenden der Biologie und Medizin gedacht. Es ist in deutscher Sprache abgefaßt. Aus der kaum noch überschaubaren Literatur wurden über 350 Zitate ausgewählt, die teilweise noch weitere Übersichten enthalten. In allen Abschnitten bietet das Heft Anregungen in dieses faszinierende Gebiet „einzusteigen“. E. Kulzer, Tübingen

Halász, N.: **The vertebrate olfactory system.** Chemical neuroanatomy, function and development. Budapest: Akadémiai Kiadó 1990. 281 S. DM 60,–. ISBN 963-05-5634-0

In diesem Buch werden morphologische und neurochemische Befunde sowie die zentralnervösen Anteile des Geruchssystems dargestellt. In einem sehr ausführlichen und mehr als 40seitigen Literaturverzeichnis werden die Quellen, auf denen der Autor seine Darstellung gründet, zusammengestellt.

Nach einer kurzen Einleitung werden die verschiedenen Ebenen des Geruchssystems besprochen. Dabei wird jeweils über die licht- und elektronenmikroskopisch untersuchbare Struktur, über biochemisch-molekulare Prozesse und gegebenenfalls auch über phylogenetische Differenzierungen berichtet. Nach Schilderung der Rezeptoren der Geruchswahrnehmung (31 S.) und der Fila olfactoria (hier „Nervus opticus“ genannt) (9 S.) folgt dann als Hauptteil des Buches auf 145 S. die Besprechung des Bulbus olfactorius. Die Zytoarchitektonik, die synaptische Organisation, die Glia-Anteile, die chemischen Differenzierungen, wie auch funktionelle und ontogenetische Aspekte werden für den Bulbus olfactorius ausführlich geschildert, und auch die Plastizität dieser Struktur wird besprochen.

Der Tractus olfactorius, übergeordnete olfaktorische Zentren und akzessorische Systeme, wie beispielsweise das Vomeronasal- oder Jacobson'sche Organ werden in kurzen Abschnitten vorgestellt. Wenn auch in diesem Buch strukturelle und neurochemische Gesichtspunkte den Schwerpunkt der Betrachtungen bilden, so wird doch kurz auf sechs Seiten die verhaltensbiologische Bedeutung des Geruchssystems bei Vertebraten dargestellt, wobei besonders die Entdeckung und Unterscheidung von Geruchsstoffen sowie das Erlernen und Erinnern von Geruchsqualitäten und deren Bedeutung für Ernährung und Fortpflanzung berücksichtigt werden. Ein achtseitiges Kapitel, welches sich mit der Bedeutung des Geruchssystems für den Menschen beschäftigt, schließt den Text ab.

Die Fülle der Daten wird durch einen etwa zehnseitigen Index erschlossen, und das Buch kann mit seiner Hilfe als Nachschlagewerk genutzt werden. P. Langer, Gießen

Piechocki, R.: **Die Wildkatze.** Neue Brehm-Bücherei 189. Wittenberg Lutherstadt: A. Ziemsen 1990. 232 S., 98 Abb., 26 Tab. DM 30,50. ISBN 3-7403-0226-7

Rudolf Piechocki, der Autor dieser Neuerscheinung aus der Neuen Brehm-Bücherei, hegt seit seiner Jugend ein leidenschaftliches Interesse für die Waldwildkatze, *Felis silvestris silvestris*. Dementsprechend konnte er während seiner langjährigen Tätigkeit am Zoologischen Institut in Halle viele Daten und Materialien über diese versteckt lebende Säugerart zusammentragen und bearbeiten. In dieser Artmonographie faßt er alte, überlieferte Angaben mit neueren aus dem gesamten Verbreitungsgebiet und eigenen Untersuchungsergebnissen an regionalen Vorkommen (über 100 Individuen) zusammen. Das Büchlein ist inhaltlich gegliedert in die Abschnitte: Einleitung, Benennung, fossil belegtes Vorkommen, Systematik, Verbreitung in Europa, Morphologie und Anatomie, Biologie und Ökologie, Schutz und Hege, Literatur, Register.

Sehr ausführlich wird auf 62 Seiten die heutige vermutete und auch nachgewiesene Verbreitung in den verschiedenen europäischen Ländern dokumentiert, besonders genau für die alten Bundesländer

und das Gebiet der damaligen DDR. Nachweise in Form von Direktbeobachtungen, Spuren, Totfunden, Fängen etc. werden häufig mit Orts- und Zeitangaben belegt. Morphologische und anatomische Besonderheiten werden dann auf 48 Seiten beschrieben und in Maßen und Gewichten mit statistischen Sicherungen mitgeteilt. Hier wird auch auf Unterscheidungsmerkmale zwischen Wild- und Hauskatze und das Erkennen von Blendlingen näher eingegangen.

Das Kapitel über Biologie und Ökologie (68 S.) ist ebenfalls sehr informativ, obwohl gerade hier viele Fragen unsicher oder gar nicht beantwortet werden können. Die Darstellungen vieler Einzelbeobachtungen enthalten zum Teil recht abweichende Angaben über Habitatsansprüche, Reviergrößen und Dichten. Über das Verhalten im Territorium ist kaum etwas bekannt, und auch ein Aktivitätsrhythmus ist nur unter Bedingungen von Gefangenschaftshaltung erstellt, aus der freien Natur jedoch nur ungenau bekannt. Telemetrische Untersuchungen an mehreren Individuen wurden bislang nur in Ansätzen in Schottland und Lothringen durchgeführt. Die Angaben zur Fortpflanzungsbiologie entstammen ebenfalls fast ausschließlich Beobachtungen aus zoologischen Gärten. Geschlechtsreife vor Erreichen des 1. Lebensjahres, Ranz im Februar–März und mittlere Tragzeit von 68 Tagen (63–70) scheinen arttypisch. Für Schottland, Mitteleuropa und den Kaukasus wird eine zweite Brunft im Hochsommer angeführt, in Ausnahmen sogar eine dritte.

Insgesamt liegt eine umfassende Dokumentation vor mit vielen anekdotenhaften Schilderungen und Einzelbeobachtungen belebt, allerdings nicht frei von mehreren Wiederholungen. Die Tatsache, daß bei Wild- und Haustierform der Katze mehrfach von zwei Arten gesprochen wird, ist allerdings aus zoologischer Sicht störend.

D. Kruska, Kiel

Vander Wall, S. B.: **Food hoarding in animals.** Chicago and London: The University of Chicago Press 1990. 445 S., Abb., Tab. Kart. $ 34.50. ISBN 0-226-84735-7

Futterspeichern kommt bei Säugetieren (vor allem Insektenfressern, Raub- und Nagetieren), Vögeln (besonders Greifvögeln, Eulen, Kleibern, Meisen und Corviden) und Arthropoden (Spinnen, Käfern, Hautflüglern) vor, wobei Sammlen jeglicher Nahrung, die zu künftigem Gebrauch gehandhabt wird, unter diesen Begriff fällt. Der Autor, der sich vor allem mit dem Anlegen von Vorräten bei Corviden, in erster Linie amerikanischen Tannenhähern, befaßt hat, behandelt die Art, Verteilung und Liegedauer von Vorräten, wie sie vor Entdeckung durch Konkurrenten geschützt und vom Besitzer wiedergefunden werden, welche Vor- und Nachteile mit ihrer Anlage verbunden sind und unter welchen Umständen Futterspeichern in der Evolution entstanden sein könnte. Reizvoll ist hier besonders die Koevolution zwischen Futterspendern (*Pinus*-Arten) und ihren Nutznießern (Tannenhähern) und die Rolle von Samen versteckenden Tieren für die Verbreitung bestimmter Pflanzenarten. Beispiele für die innerartliche geographische Variabilität der Sammeltätigkeit, für Unterschiede im Jahreslauf oder zwischen den Geschlechtern und Futterarten werden behandelt. Die Sammelbereitschaft ist bei Weidenmeisen wie Waldmäusen im Kurztag groß, im Langtag gering und wird offensichtlich über den Einfluß der Fotoperiode auf die Sexualhormon-Produktion gesteuert. Bei Laborratten wurden Abnahme der Eintragebereitschaft mit zunehmender Temperatur und wachsendem Körpergewicht registriert. Spezielle Kapitel besprechen die futterspeichernden Arten in systematischer Folge. Obwohl im Schriften-Verzeichnis etwa 1500 verwertete Zitate aufgeführt werden, sind noch viele Fragen offen. Das hängt sicherlich mit der großen Variabilität von Speicherverhalten und der Schwierigkeit zusammen, Vorräte in der Natur aufzufinden, bestimmten Individuen zuzuordnen und die Nutzungsrate zu ermitteln, um nur einige vordergründig zu erfassende Daten zu nennen. Zudem ist es oft schwer zu entscheiden und eine Frage der Interpretation, ob nicht sofort verzehrtes Futter, als Vorrat gewertet wird, wie Tab. 9.4 über die Eulen zeigt. Danach hätte *Bubo virginianus* Nager und Hasen, *Bubo bubo* und *Athene noctua* nonpasserine Vögel „gespeichert". Dies deutet auf einmalige, nicht generalisierbare Feststellungen.

Schlecht ausgewertet ist die europäische und vor allem deutschsprachige Literatur. Der Feldhamster (*Cricetus cricetus*), Inbegriff des Vorratsspeicherers unter den Nagetieren, wird nur einmal auf S. 263 unter Hinweis auf Nowak und Paradiso (1983), eine Sekundärquelle, kurz erwähnt. Auf der gleichen Seite wird behauptet, der deutsche Name „Hamster" sei vom Verb „hamstern" abzuleiten. Es dürfte wohl umgekehrt sein. Ähnlich dürftig sind die Bemerkungen etwa über Gliriden. *Arvicola* kommt namentlich überhaupt nicht vor. Diese Mängel ungeachtet, lohnt sich die Anschaffung des Buches, das insgesamt vielseitig, anregend, gut verständlich, wohl geordnet und ansprechend bebildert ist.

J. Niethammer, Bonn

Peters, G.; Hutterer, R. (eds.): **Vertebrates in the Tropics.** Bonn: Zoologisches Forschungsinstitut und Museum Alexander Koenig 1990. 424 pp., soft-bound, numerous illustrations and tables. DM 85,– (including postage). ISBN 3-925382-32-1

This book publishes the "Proceedings of the International Symposium on Vertebrate Biogeography and Systematics in the Tropics" held in Bonn, June 5–8, 1989. It contains 33 chapters, of which 12 refer exclusively to mammals. Some of the other articles present reviews that deal with vertebrates in

general and to a minor extent also refer to mammals. Each paper starts with an abstract and gives a list of relevant literature. Thus, efficient overviews and introductions are presented.

After short introductory remarks of the editors, four chapters deal with the paleontology and paleobiogeography in the tropics. In one of the chapters STORCH discusses the paleogeographical jigsaw puzzle of the Eocene mammalian fauna from Messel near Darmstadt. HAFFER presents aspects of allopatric speciation and also considers mammalian taxa.

The following part of the book, consisting of six chapters, presents "New Data and Discoveries". In one of the chapters HUTTERER and YALDEN introduce two new shrew species from Ethiopian relic forests and two other papers deal with rodents: VAN DER STRAETEN and DUDU comment on *Praomys* from Zaire and ALBERICO on geomyids from South America.

The most extensive section of the book, consisting of 21 chapters, deals with "Patterns, Analyses and Models". There are generalizing articles that cover mammals from Angola (FEILER), the Philippines (HEANEY and RICKART) and Peru (PATTON et al.). CLAESSEN and DE VREE deal with the chiropteran genus *Epomophorus* that has a wide distribution in tropical Africa. Results of electrophoretic studies on *Crocidura* are presented by MADDALENA, and HUTTERER and TRANIER discuss the immigration of *Suncus murinus* into Africa and Madagascar. DIETERLEN deals with rodents of the African rain forest and in a very informatively illustrated contribution GRUBB gives an excellent introduction into "Primate geography in the Afrotropical forest biome".

A final chapter by SAYER et al. deals with the necessity of conservation of vertebrate diversity in tropical forests through appropriate management.

The well-produced book includes many informative illustrations and a wealth of data that – in some cases – are presented in extensive tables as appendices to their articles. This publication is a useful source of information for those zoologists that are interested in tropical vertebrates.

P. LANGER, Gießen

KINGDON, J. **Island Africa.** The Evolution of Africa's Rare Animals and Plants. London: Collins 1990. 287 pp., num. figs. £ 25.00. ISBN 00-219-443-0.

Amongst mammalogists, JONATHAN KINGDON needs no introduction since his monumental seven volume work on East African mammals has become an invaluable source of reference. Several exhibitions of his animal drawings and paintings in London and Oxford (in Germany at Gießen and later in the Senckenberg Museum of Frankfurt) have aroused both academic and public interest.

His new book provides a platform for the Tanganyika-born artist and biologist from which he makes his plea for unique, rare or endangered animal and plant species. He offers his synoptic view of Africa's flora and fauna which he follows through a series of ecological "islands". With the artist's eye, supported by admirable knowledge of taxonomic and functional relationships, he uncovers evolutionary processes and dependencies, which the expanding species *Homo sapiens* threatens to disrupt forever. KINGDON's concentrated expeditions through unique African ecosystems are aesthetic and scientific eye-openers demanding our active participation in realistic conservation concepts.

The generously illustrated book follows an endemism concept which the author displays in 13 chapters, each consisting of a biogeographic example which he treats like treasures (e.g., Horn of Africa, Zaire basin – "an evolutionary whirlpool" etc.). He proposes new strategies, lists endemic species, reserves and parks in appendices – whoever is engaged in scientific work in Africa should study KINGDON's "Islands".

R. R. HOFMANN, Gießen

OORSCHOT, D. E.; JONES, D. G.: **Axonal Regeneration in the Mammalian Central Nervous System.** A Critique of Hypotheses. Advances in Anatomy, Embryology and Cell Biology. Vol. 119. Berlin, Heidelberg, New York, London, Paris, Tokyo and Hong Kong: Springer Verlag 1990. 121 pp., 38 figs, 17 tabs. DM 89,–. ISBN 0-387-51757-X

In contrast to other tissues, the central nervous system (CNS) has very limited possibilities to regenerate after injury. Axonal regeneration is such a possibility and thus its explanation is a problem of scientific and practical relevance and a large amount of papers is dealing with this phenomenon. In four chapters the authors present 1. a survey on hypotheses, 2. in vivo experiments and 3. in vitro experiments to explain regeneration in the CNS before they come to 4. conclusions. It is pointed out that many hypotheses which try to explain the failure of the CNS to regenerate as other tissue does, lack sufficient experimental verification. Thus, in vitro experimental approaches are discussed as a possibility to help solving this problem. Finally five hypotheses are presented "as the most worthy of consideration in enhancing the CNS regenerative response. These are the proliferation of non-neuronal cells, incompatibility between neuronal and non-neuronal cells, vascular permeability, the absence of specific growth factors and the somal response". None of these hypotheses is said to explain alone the regenerative response, but taking together parts of these hypotheses would help to gain further insights.

The review of OORSCHOT and JONES is a very useful survey not only for those, who are engaged scientifically into this problem, but also for neurobiologists in general.

G. REHKÄMPER, Köln

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers, PO Box 1815, New York, NY 10156-0610, USA. Phone (212) 679–0782, Telefax (212) 213–3798.

Erscheinungsweise und Bezugspreis 1992: 6 Hefte bilden einen Band. Jahresabonnement Inland: 358,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 351,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 358,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

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Fortsetzung 3. Umschlagseite



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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

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Pelage variation in *Marmosa incana* (Didelphidae, Marsupialia) with notes on taxonomy

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Abstract

Described and analysed pelage patterns of *Marmosa incana*, on the basis of museum specimens over the whole geographic range of the species. Three pelage types were identified by the length and texture of the dorsal hairs. Consistent occurrence of these pelage types in different age and sex classes along the year refute previous hypotheses of geographic variation and pelage seasonality and point to an intrinsic determination of the pelage types. The taxonomic status of the forms formerly included in Tate's (1933) *incana* section is discussed and possible causes of sexual dimorphism in pelage are surveyed.

Introduction

With forty-seven recognized species (Honacki et al. 1982), the genus *Marmosa* is the most diverse taxon of Neotropical marsupials. In Tate's (1933) classical revision the genus *Marmosa* was defined comprising five major species groups, each one subdivided in sections. Although recent authors (e.g. Pine 1972; Kirsch 1977) have suggested that *Marmosa* could be split into different genera, this taxon has remained undivided, as formerly claimed by Tate, except by the brief proposition of Gardner and Creighton (1989), in which *Marmosa* (s. l.) was divided in five genera coincident to a great extent with the five species groups of Tate (1933). At the specific and subspecific levels the study of Tate (1933) remains the only detailed description of the variation in *Marmosa*, especially in what concerns the forms analysed in the present study. For this reason, Tate's (1933) assignment of species and species groups will be followed hereafter.

The *incana* section of Tate's (1933) *noctivaga* group comprises two species that occur in eastern Brazil: *Marmosa incana* (Lund, 1841), which is the genotype of the genus *Marmosops* according to Gardner and Creighton (1989), and *M. scapulata* (Burmeister, 1856). These two forms are mainly distinguished by the presence of conspicuous stiffened hairs in the scapular regions of the latter species. In addition to the modified pelage of *M. scapulata*, Tate (1933) also identified sexually dimorphic long and short pelages to characterize subspecies of *Marmosa incana*. In a recent interpretation of the same pelage variation, Emmons (1990) identified the long and short furs of *Marmosops incanus* as seasonal coats, and ascribed a third pattern showing a "collar" of new hair to a molt stage.

The first intend of this study is to bring a more comprehensive description of pelage patterns in the *incana* section. In order to understand the determinants of the pelage variation we also analyse the occurrence of the pelage patterns in relation to age, sexual and seasonal variation.

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Material and methods

A total of 311 museum specimens was analysed in this study. Localities, sample sizes, and museum acronyms are as follows: MN = Museu Nacional, Rio de Janeiro; UFMG = Departamento de Zoologia, Universidade Federal de Minas Gerais; MBML = Museu de Biologia Mello-Leitão; MHNCI = Museu de História Natural "Capão da Imbuia".

Bahia: Feira de Santana (1, MN); Ilhéus (83, MN); Jaguaquara (2, MN); Jequié (3, MN); Serrinha (6, MN). – Minas Gerais: Além Paraíba (64, MN); Almenara (1, UFMG); Caratinga (1, UFMG); Conceição do Mato Dentro (9, MN); Grão Mogol (5, MN); Juíz de Fora (6, MN); Lagoa Santa (15, MN); Parque do Ibitipoca, Lima Duarte (1, UFMG); Mocambinho, Manga (8, MN); Parque Florestal do Rio Doce, Marliéria (4, UFMG); Ponte Nova (2, MN); Caraça, Santa Bárbara (21, UFMG); Rio Casca (1, UFMG); Sete Lagoas (3, UFMG); Várzea da Palma, Serra (2, UFMG); Parque Nacional da Serra da Canastra (1, UFMG); Turmalina (1, MN) Vargem da Lapa (2, UFMG); Volta Grande (6, MN). – Espírito Santo: Campinho (1, MN); Cariacica (6, MBML); Castelo (3, MBML); Nova Lombardia (1, MN); Santa Tereza (13, MBML). – Rio de Janeiro: Ilha Grande, Angra dos Reis (4, MN); Poço das Antas, Silva Jardim (2, MN); São João Marcos (1, MN); Teresópolis (10, MN); Tijuca, Rio de Janeiro (5, MN); Tinguá, Nova Iguassu (1, MN). – Paraná: Piraquara (2, MHNCI). – No locality: (14, MN).

Date of collecting and sex were obtained from original tags. In order to determine the age of specimens we used a modification of the system proposed by Tribe (1990) which is based on the sequence of eruption of molariform teeth (classes 1 to 6) and wearing of M4 (classes 6 and 7). We noted that the angle of placement of M4 is individually variable, sometimes resulting in abnormal wearing of this tooth. Consequently, we analysed additional wearing of M1–M3. Beginning of class 6 is readily identifiable by incompletely erupted PM3; to classify individuals with fully erupted PM3, scores were attributed to three consecutive stages of M1–M4 wearing, the first being posteriorly allocated to age classe 6 and the last two stages to age class 7 (7^{I} and 7^{II}).

Types of pelage were identified on the basis of length and texture of dorsal fur. Medium pelage

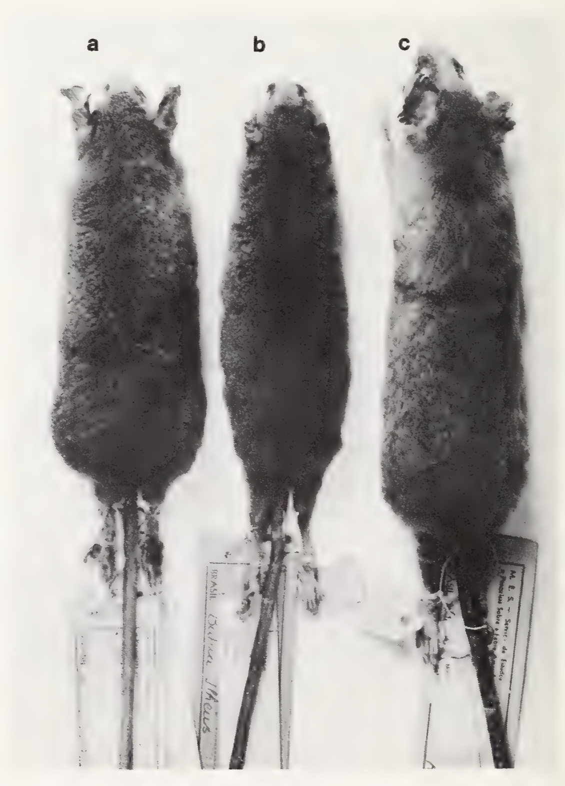


Fig. 1. Dorsal view of individuals of each pelage pattern described. a: type A; b: type B; c: type C

length was measured with a millimetric ruler at the mid-dorsum of each specimen. The texture was estimated by touch and classified in soft, coarse and stiffened categories. Hairs from the back, scapular and throat region of representative individuals of each sex and pelage pattern were observed under a binocular microscope with a drawing tube to assess gross morphologic differences and to draw the distinct hair types.

Samples from states of Bahia, Minas Gerais and from combined localities from the states of Rio de Janeiro, Espírito Santo and Paraná, congruent with geographical distances and ranges of the subspecies of *M. incana* proposed by Tate (1933), were examined separately. Distributions of pelage patterns by age, sex and month were found to be similar in the three samples, but the respective sample sizes became much reduced when analysed monthly. Therefore, we tabulated the frequencies at each pelage pattern by age, sex and by month for all specimens. Animals that had been kept in captivity were excluded from the analyses.

The occurrence of an orange to rust brown stain around the mammary area is an indication of pregnancy and nursing (Barnes 1977), and was used to determine reproductive status in females. Reproductive condition in males is more difficult to determine from external markings, and was assessed by histological examination of testes for spermatogenic activity in two available males (MN 29 006 and MN 29 007).

Results

The following three patterns were identified in the analysis of the hairs of the back. Type A (Fig. 1a) shows a uniform dorsal fur, shiny, brownish gray, with soft and long hairs, length 8–12 mm (Fig. 2a). In type B (Fig. 1b) the dorsal pelage is also uniform and brownish gray, but coarse, dull and short, hairs length 5–8 mm (Fig. 2b). The most conspicuous pattern, type C (Fig. 1c), exhibits an heterogeneous dorsal coat: the scapular region shows modified broadened and stiffened yellowish hairs, length 5 mm (Fig. 2c), extending backwards, reaching the mid-dorsal region in some specimens. In the interscapular area the fur is shorter (4 to 9 mm long) and dull grayish, with some modified hairs mixed to the normal ones; the remainder dorsal pelage is similar to type A, with hairs 10 to 12 mm long.



Fig. 2. Hair types associated with each pelage pattern. a: dorsal hair of pelage types A and C; b: dorsal hair of pelage type B; c: scapular hair of pelage type C

Pelage type A comprises individuals ranging from age classes 3 (the younger individuals of our sample) to 6 in both sexes, as well as 61 % of the males of age class 7^{I} (Fig. 3). Only females showed pelage type B, which occurred in 13 % of the individuals of age class 6, and in the entire age class 7 (7^{I} and 7^{II}). Pelage type C was found only among males, in 6 % of age class 6, 39 % of age class 7^{I} and 100 % of age class 7^{II}.

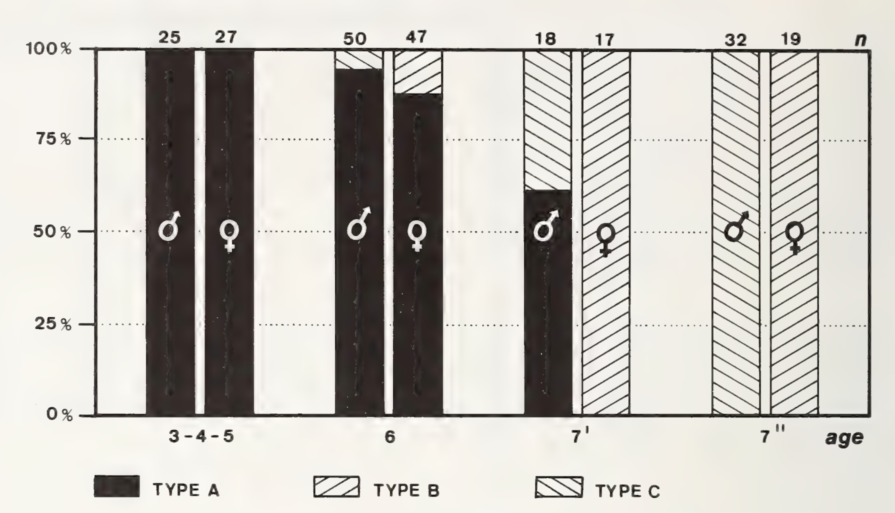


Fig. 3. Frequency (percent) of pelage patterns by age classes

The ventral pelage is ivory white in the three patterns described, with soft and long hairs in type A and C, whereas short and coarse in type B. In the throat region all males of pelage type C show modified hairs similar to that of the scapular region. In pelage type A, although occupying a much smaller area, the modified throat hairs are also present in 12 % (n = 6) of the individuals of age class 6 and in 40 % (n = 4) of age class 7.

In four males (MN 8296, 11 147, 13 367 and 24 684) of pelage type A and age classes 6 and 7^{I}, we observed a very small area of modified stiffened hairs on both sides of the neck, near the scapular region. One class 7^{I} female (MN 17 158) showed an atypical condition of pelage with venter and anterior half of dorsum with pelage type B and posterior half with pelage type A. This pattern was also found in another female specimen (MN 11 157, skin only).

Tabulation of the occurrence of pelage patterns by month (Fig. 4) reveals that type A occurs throughout the year, more often from January to August and decreases toward the end of the year. Pelage type B shows low frequencies between January and July, and shows higher frequencies from September to November. Type C is seldom present from February to May and its frequency increases from July on.

Discussion

Pelage patterns

The patterns of pelage identified here have already been partially described in the literature. Type A is the most often mentioned, possibly because it is the most common in nature, occurring in both sexes from age class 3 (at least) to age class 6. This is the basic pelage pattern of *Marmosa incana* according to TATE (1933), reported for both sexes of *M. incana paulensis* and for males of *M. incana bahiensis* and *M. incana incana*. This pelage type was referred to by EMMONS (1990) as the winter coat, occurring from May to August.

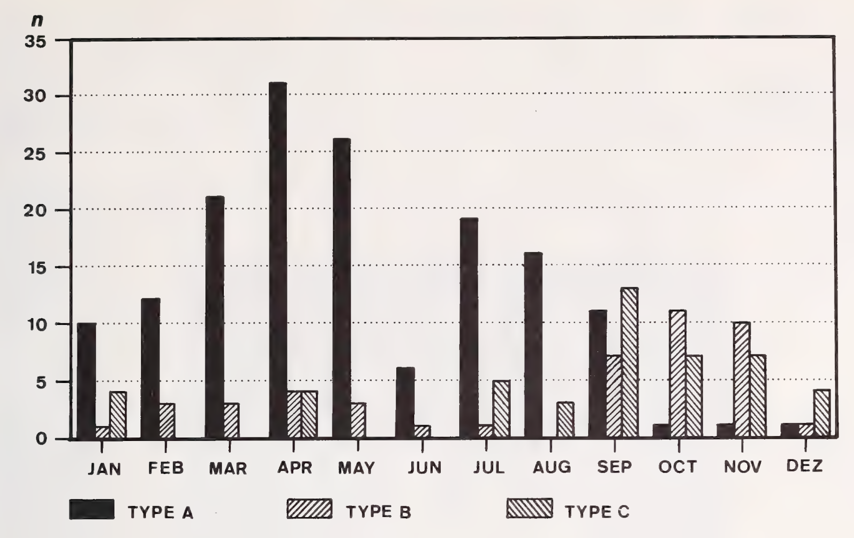


Fig. 4. Frequency of pelage patterns by month

TATE (1933) was the first to identify pelage type B, and related it to females of *M. incana incana* and *M. incana bahiensis.* EMMONS (1990) described this short fur as a summer coat, occurring between January and April.

Pelage type C was first reported in the description of *Grymaeomys scapulatus* Burmeister, 1856, which is *Marmosa scapulata* for TATE (1933). EMMONS (1990) suggested that this pattern represents a moult stage between the summer and winter coats in *Marmosops incanus,* restricted from September to December, and pointed out that it was once described as a different species.

Our results do not indicate that pelage types A and B are alternate seasonal coats. Although pelage type A exhibited higher frequencies between January and August and type B was more common between September and December, we find types A and B concomitantly distributed along all the year. Moreover, absence of pelage type A among individuals exhibiting accentuated molar wearing (age class 7^{II}) and absence of pelage types B and C among individuals of age classes 3, 4, and 5 throughout the year are evidence that the change from long (type A) to short (type B) fur is a single and definitive event.

We have evidence, nevertheless, for a transition from pelage type A to B and from A to C. The six specimens stressed above, four males with incipient stiffened scapular pelage and the two females with short/long dorsal pelage, are thought to represent intermediate conditions between pelage types A und C and types A and B, respectively. These specimens were collected between August and September (males) and between September and October (females), periods in which we notice an inversion in the ratios between frequencies of pelage types A/C and A/B in the year (Fig. 4).

In contrast, ordinary moulting is represented in our sample in seven individuals of pelage type A, which show an incipient layer of new soft hairs under the long dorsal hairs. Close inspection of the associated hairs did not reveal the stiffened characteristic hair of type C, nor the individuals in moult were restricted to a determined part of the year.

In regard to the relation between sex and pelage, our results also do not corroborate the assertion by TATE (1933) that the long (type A) and short (type B) pelages are sexually dimorphic furs. In fact, type A represents the monomorphic pelage for both sexes, occurring from age 3 to 6. On the other hand, the available data demonstrate that pelage types B and C are related to secondary sexual dimorphism in the *incana* section. There is

also an apparent association between these pelage patterns and sexual maturity. Only pelage type B females showed the stained mammary region, which is an indication of reproductive activity. As for the males, it is interesting to note that the individuals of pelage type A examined, although as old as age class 7, did not show any spermatogenic activity. It seems, therefore, that pelage type C is achieved in concern with the sexual maturity.

These results indicate that the pelage patterns described represent distinct age and sex related stages in all studied populations of the *incana* section. Whereas only the age component is responsable for the distinct pelages of youngs and sub-adults, the age, sex and sexual maturity determine the dimorphic adult pelages B (females) and C (males). The "seasonal" component is but a function of different age fluctuations along the year, and cannot account for the determination of pelage variation in the *incana* section.

Taxonomic remarks

Some taxonomic implications result from the conclusion above. The modified scapular pelage, diagnostic of *Marmosa scapulata,* is in fact the adult (maturated) male pelage observed in all populations of the *incana* section. Therefore, *Grymaeomys scapulatus* Burmeister, 1856, is a subjective junior synonym of *Marmosa incana* (Lund, 1841). The fact that adult males of *M. incana* match the *M. scapulata* pelage pattern was already noted by Tribe (1987), who pointed out a possible conspecifity of these two forms.

Examining the holotype of *M. scapulata* (Berlin Museum 2330) Tate (1933) verified that the skin was faded to light brownish. In Burmeister's (1856) original description, hairs were "at base slate gray, then pale yellow-red, and last cinnamon". This banding pattern agrees very closely to that we found in specimens of *M. incana,* and results in a grayish dorsal colour, brownish washed above.

Tate (1933) was the first to recognize the close relationship between *M. scapulata* and *M. incana,* and notwithstanding cranial and distributional similarities between these taxa, the pelage differences convinced him of the distinctiveness of *M. scapulata.* Apparently, no male skins of age class 7^{II} (where all males show pelage type C) were available to Tate (1933). Noteworthly, the only male specimen of *Marmosa incana* referred by Tate (1933) to be very old (Copenhagen 132) had no skin. This insufficient sample probably contributed to the recognition of *M. scapulata* as a full species.

In his review, Tate (1933) recognized three subspecies of *Marmosa incana,* based mainly on pelage traits. *Marmosa incana incana* and *M. incana baihensis,* characterized by sexual dimorphism in pelage length (short in females and long in males) differed by the presence of gular stiffened hairs in males of the former subspecies. These forms were distinguished from *M. i. paulensis* in which both sexes showed long fur (type A). In our study, which covers the total geographic range of *M. incana,* and includes topotypic series of *M. incana incana* and *M. incana paulensis,* the pelage type B (short fur) and the gular stiffened hairs in males are present in all subsamples in some individuals of classes 6 and 7^{I} and in all representatives of age class 7^{II}. Consequently, as far as pelage is concerned, the subspecific structure of *M. incana* proposed by Tate (1933) is inconsistent and should be reconsidered, because it is based on age rather than on geographical differences. Apparently, the pelage diagnoses proposed by Tate (1933) for the subspecies of *Marmosa incana* result from young-biased samples of the populations described as *M. i. bahiensis* and *M. i. paulensis* in relation to the nominal subspecies.

Sexual dimorphism

A further implication of our study relates to sexual dimorphism in pelage in *M. incana.* Pelage of adult males (type C) differs strikingly from that of adult females (type B), juveniles,

and subadults (type A). A less conspicuous difference is found between adult females and younger individuals of both sexes. As far as we know this is the first marsupial to show sexual dimorphism in pelage structure.

According to Ralls (1977), sexual selection is the most important mechanism affecting male's colour and structures used in displays. Although territorial and reproductive behavior in *M. incana* is unknown, the modified scapular pelage in males with upstanding, self-coloured and frontally positioned hairs (Fig. 5) may perform a role in social interactions among adult individuals, and could be related to sexual selection.



Fig. 5. Live adult male of *Marmosa incana* showing pelage type C. Note darker line formed by the gray bases of longer hairs adjacent to the modified scapular pelage

Apparently, the occurrence of differentiated adult pelage has not been referred to in female mammals. This may be due to either extreme rarity of this phenomenon in the wild, or to overshadowing by relatively greater distinctiveness of males. In the case of *M. incana,* the differentiated pelage type B could be a consequence of epigenetic interactions hindering the full manifestation on females of a fixed male trait. An alternative hypothesis would deal with selection upon pelage in females, the short fur possibly representing an advantage either in the heat improvement to the young in the teat attachment phase, or in the recognition of the female reproductive status. At any rate, the actual causes of the differentiated female pelage remain to be demonstrated.

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Zusammenfassung

Variation des Haarkleides von Marmosa incana (Didelphidae, Marsupialia) mit Anmerkungen zur Taxonomie

Die Haarkleider der südamerikanischen Beutelratte *Marmosa incana* werden beschrieben; nach der Länge und der Struktur der Rückenhaare können drei verschiedene Haarkleider (A, B, C) unterschieden werden. Alle drei Kleider treten zu fast jeder Jahreszeit auf; dies widerspricht früheren Theorien, die von geographischer Variation oder einem saisonalen Haarkleidwechsel ausgingen. Statt dessen besteht offenbar eine Relation zwischen dem Auftreten von Haarkleid B und der sexuellen Aktivität der Weibchen und dem von Haarkleid C und der sexuellen Aktivität der Männchen. Auf der Grundlage der neuen Befunde wird die Taxonomie verschiedener Formen der *incana*-Gruppe von Tate (1933) diskutiert, und die möglichen Ursachen eines Sexualdimorphismus im Haarkleid von Säugetieren werden besprochen.

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Characteristics and distribution of breeding dens of the Red fox *(Vulpes vulpes)* in a mountainous habitat

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Abstract

Described the red fox breeding dens of a 30 km^2 area and compared them to the non-breeding dens. Dens were searched and controlled since 1986. In 1990 every den was characterized to examine their distribution and characteristics. The total number of dens was 62 (0.33/km^2). 19.4 % of them were used for cubbing (1.88/km^2). No significant difference in the characteristics of breeding and non-breeding dens was found except for the number of entrances, which was higher in the breeding dens. Man-made structures could be used as breeding dens as well as dens dug by badgers. The breeding dens were not further distant from roads and houses than the other dens. The breeding dens were not evenly spaced in the area and the same ones were generally used over several years. Results showed that the use and distribution of breeding dens was limited by the number of suitable sites. The number of breeding dens could be used to estimate the number of foxes in an area but this requires information on the social organization of the special fox population.

Introduction

Dens are used by the red fox *Vulpes vulpes* for two different activities: 1. as resting sites during the non-active period (non-breeding dens), 2. as sites for birth and rearing of cubs (breeding dens). Some dens are used for both activities. Several papers have described the characteristics of fox dens in different habitats (e.g. Fuchs 1973; Eiberle 1975; Weber 1983; Roman 1984; Iokem 1985; Paquot and Libois 1986), but there are only few data on breeding dens (Hewson 1986; Nakazono and Ono 1987; Brochier 1989). The question of breeding dens is important because it could provide useful information about a fox population, i.e., number of foxes, recruitment, and level of urbanization. In this paper we compare some characteristics of the breeding dens with the non-breeding dens, and show their distribution and use, using data obtained in a mountainous area in Switzerland.

Material and methods

Since 1989 and after a preliminary study of three years (Paratte 1989) we monitored the fox population of a 30 km^2 area in the Swiss Jura Mountains. The study area is described in Weber et al. (1991). The relief is karstic and the soils are shallow and unsuitable for burrowing, except in some small areas with peat. Roads and farms are numerous and evenly spaced.

Dens were found by walking systematically throughout the study area, using fox tracks in the snow during winter. Starting in March, every den was controlled every week in order to assess the presence of cubs. The occupation of a den by a fox family was confirmed by direct observation. In summer 1990, we checked every known den or den site in order to study their distribution and their characteristics. Each one was characterized using:

1. The type of habitat. Four categories were distinguished:
   forest (20.1 % of the study area), wooded pasture (25.2 %), pasture (31.9 %), and fertilized meadow (22.8 %). For "forest" two subcategories were made: "forest" and "forest's edge".
2. The type of substratum. The different possibilities were:
   a) den dug in the earth among spruce root system ("spruce root system") by foxes or badgers;

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b) den dug in bare earth ("earth"); c) den situated in rocks ("rocks"); d) den situated in dumping-grounds, man-made accumulations of stones, wood, fire proof garbadges, ... ("dumping-ground"); e) combinations between these four categories: i.e., den with some entrances in the earth among spruce root system and some in bare earth ("spruce root system/earth").
3. The number of entrances: N.
4. The distance to the nearest road (main roads only) D_R.
5. The distance to the nearest house: D_H.
6. The distance to the nearest breeding den (for breeding dens only).

To test the distribution of the breeding dens, we compared the observed nearest distances between breeding dens with the nearest distances obtained by a simulation programme which set 12 points randomly (with the same probability for each surface unit) on the surface corresponding to the study area. Simulation was repeated 1500 times.

Results

Number and density

In spring 1990, the total number of dens regularly used by foxes in the study area was 62. Twelve of them (19.4 %) were used by 11 fox families as breeding dens: one family having moved, one week after the first emergence of cubs, to another den. Counting only one den for this family, the density of dens was therefore 1.88/km^2 and for breeding dens 0.33/km^2 (Fig. 1).



Fig. 1. Location of the dens in the study area in 1990. ▬▬: major road; ——: secondary road; △△△: limits of the study area; ★: breeding dens; ●: non-breeding dens; spotted: wooded areas

Characteristics

Six of the 12 breeding dens were situated in forests, all within 10 to 80 m of the edge, 3 immediately on the edge of forest, and 3 in wooded pastures. This situation did not differ from the location of the non-breeding dens (Fisher exact probability test, $p > 0.05$), (Table 1). Comparison of observed number of dens and expected number of dens in the different habitats showed a clear preference for covered areas: forests and wooded pastures (Table 2).

Table 1. **Comparison of the location of breeding and non-breeding dens**

	Breeding dens (N = 12)	Non-breeding dens (N = 50)	Fisher test
Forest	6 (50 %)	17 (34 %)	n.s.
Wooded pastures	3 (25 %)	25 (50 %)	n.s.
Pastures	0 (0 %)	3 (6 %)	n.s.
Forest edge	3 (25 %)	5 (10 %)	n.s.

Table 2. **Comparison of observed den locations with expected den locations**

Habitat and proportion (%) of study area	Breeding dens (N = 12)			Non-breeding dens (N = 50)		
	obs.	exp.	Binomial test	obs.	exp.	Binomial test
Forests (20.1 %)	9	2	p < 0.05	22	10	p < 0.05
Wooded pastures (25.2 %)	3	3	n.s.	25	13	p < 0.05
Pastures (31.9 %)	0	4	p < 0.05	3	16	p < 0.05
Fertilized Meadows (22.8 %)	0	3	n.s.	0	11	p < 0.05

obs. = observed; exp. = expected.

Most of the breeding dens (57.1 %) were situated in "spruce root system/earth" substratum; the proportion of the non-breeding dens in this category was lower (Fisher test, $p < 0.05$). Other substrata were "rocks/earth", "dumping-ground", or "spruce root system" (Table 3). Two breeding dens were a complex of two dens situated at a distance of 30 m and 80 m, respectively, and used simultaneously by the family (this explains the N = 14 in Table 3).

Table 3. **Comparison of the substratum of breeding and non-breeding dens**

	Breeding dens (N = 14)	Non-breeding dens (N = 50)	Fisher test
"Spruce roots system"	1 (7.1 %)	19 (38 %)	p < 0.05
"Rocks"	1 (7.1 %)	16 (32 %)	n.s.
"Spruce root system/earth"	8 (57.2 %)	9 (18 %)	p < 0.05
"Rocks/earth"	1 (7.1 %)	2 (4 %)	n.s.
"Dumping-ground"	3 (21.5 %)	2 (4 %)	n.s.
"Rocks/dumping-ground"	0 (0 %)	1 (2 %)	n.s.
"Spruce root system/rocks"	0 (0 %)	1 (2 %)	n.s.

All breeding dens had 4 or more entrances ($4 \leq N \leq 48$), whereas 72 % of non-breeding dens had less than 4 entrances. The number of entrances was significantly greater than in non-breeding dens (Mann-Whitney U Test, $p < 0.05$). The number of entrances was related to the type of substratum: more entrances were found when digging is possible – in "spruce root system/earth", "rocks/earth" – while dens in "spruce root system" and in "rocks" had less entrances (Kruskal-Wallis One-Way ANOVA, $p < 0.05$).

Distribution

As already illustrated in Figure 1, the breeding dens in our area were not evenly but rather randomly spaced. No significant difference was found by comparing the observed and the simulated distributions (Mann-Whitney U Test, $p > 0.05$).

The breeding dens were sometimes very close to houses ($125 \text{ m} \leq D_H \leq 900 \text{ m}$) or roads ($50 \text{ m} \leq D_R \leq 750 \text{ m}$). No significant differences were observed between the breeding dens and the non-breeding dens (Mann-Whitney U Test, $p > 0.05$).

Use of breeding dens

The first signs of occupation of a breeding den were found on April 17th. Removal of 8 fox families by their parents was observed between May 16 and July 12, the disturbance sources being cattle and man. Only one family moved to an already known den (situated at a distance of 1000 m), others were seen in the breeding den area but their new den sites were not found.

Nine of the 12 breeding dens which were occupied in 1990, were also used in 1986, '87, '88, '89, or '91. Two dens were used for cubbing 5 times during the six year period. Five dens were used 3 times, and the other two twice. The number of breeding dens over the six year observation period varied from 3 (1988) to 12 (1990) (Table 4).

Table 4. **Use of breeding dens**
Data from 1986–1988 according to Paratte (1989)

	1986 N = 6	1987 N = 9	1988 N = 3	1989 N = 11	1990 N = 12	1991 N = 10
"Combes"	+++	+++		+++	+++	+++
"Assesseur"				+++	+++	+++
"Biche"		+++			+++	+++
"Tuilerie"	+++	+++	+++	+++	+++	
"Brandt Nord"	+++	+++			+++	
"Brandt Sud"					+++	+++
"Puce"				+++	+++	+++
"Robert"	+++				+++	+++
"Bousset"					+++	+++

N = total number of fox breeding dens, +++ = den used.

Discussion

Except for the number of entrances, there was no significant difference in the characteristics of breeding and non-breeding dens. The preference for covered areas was already noticed by Weber (1983), Paquot and Libois (1986) and Iokem (1985). Only Nakazono and Ono (1987) observed that foxes used dens in open land rather than in densely vegetated areas. However, there is no contradiction between these two results which

correspond to two different strategies of the fox to assure the security of the den by using either a discrete site or a site with far visibility (Artois 1989). In fact, foxes are opportunists concerning their dens. They do not dig their own dens when other possibilities are available (Weber 1983). Thus, in our area, most of the dens that had been dug were made by badgers *Meles meles* and we observed either an alternate use by foxes and badgers or, in large dens, the possibility of cohabitation. The use of man-made structures (i.e. dumping-grounds) has been reported by Weber (1983), Paquot and Libois (1986) and Brochier (1989). However, a minimum distance to human habitations (50 m) occurred in our area; no vixen chose a site for her cubs directly close to or in a house, as urban foxes have been observed to practise (Harris 1977). We noticed that, when a breeding den was close to sources of human disturbance, the site was very densely covered and the cubs emerged only at night. The high number of entrances of breeding dens seems to be a constant characteristic (Weber 1983; Nakazono and Ono 1987) and probably corresponds to the need for the cubs to escape quickly into shelter.

The difference between breeding dens and non-breeding dens in the type of substratum was due to the number of entrances. When a den in the "spruce root system" substratum (most usual non-breeding den substratum) was extended, surrounding earth could be used and the substratum became "spruce root system/earth" (most usual breeding den substratum). We emphasize that the "earth" substratum was never found: entrances were dug in bare earth, only when a den was made larger.

The observed density of breeding and non-breeding dens was lower than those observed by Fuchs (1973) in the Swiss Midland (3.5–10.8 dens/km^2). It certainly depends on fox density but also on the possibility for digging. The soils in the Jura Mountains are generally shallow. The number of breeding dens (0.33/km^2) could be qualified as "medium": it is lower than in suburban Brussels (1/km^2) (Brochier 1989) but medium compared to Great Britain (0.03–1.3/km^2) (Hewson 1986).

Hewson (1986) showed that breeding dens in different areas of Scotland were evenly spaced. Nakazono and Ono (1987) supposed the same situation in Japan. Our results are different. The difficulty for foxes to find or make an adequate den for breeding could explain the random distribution; we consider that the distribution of breeding dens was limited by the number of suitable sites.

The number of breeding dens is related to the number of breeding vixens (Nakazono and Ono 1987) and thus it is an indication of the number of foxes (Hewson 1986). However, the estimation of fox density is difficult because the number of foxes in an area also depends on the social organization of the population: foxes usually live in pairs or in groups according to area and prey availability (Artois 1989). With foxes living in groups, Brochier (1989) counted 3 individuals per breeding den to estimate the number of adult foxes.

In a stable population, the number of breeding dens should be stable (Nakazono and Ono 1987). In our area the number of breeding dens varied between years, indicating an unstable population; this fact was confirmed by night-lighting counts (Weber et al. 1991). Changes in prey availability could explain these differences. In our area, the main prey of foxes, the water vole *Arvicola terrestris*, fluctuates considerably in numbers (Weber and Aubry preliminary information). Hewson (1986) compared different habitats, and supposed that some differences in the number of breeding dens were due to food availability. However, the cycles of the water vole are pluriannual (4–8 years) and cannot be the only reason for such substantial differences in the number of dens. Although Hewson (1986) noticed no change in the number of breeding dens according to the number of foxes killed during winter, we consider that hunting pressure has an important influence on the number of breeding dens in the following year, e.g., a strong fox hunting during the winter of 1987–1988 corresponded to an unusually low number of breeding dens in the following year (Paratte 1989). Under such unstable conditions and without having established the

social organization of the population, and its possible modification, it is very difficult to make a reliable estimation of fox number using number of breeding dens.

Regular use of breeding dens over the years has already been reported by NAKAZONO and ONO (1987). Some factors could influence the use of breeding dens: number of foxes, change of the mating individuals, disturbance at the moment of birth. This fact showed once again the importance of the "pool" of breeding dens in an area. Human permanent disturbances of these sites or their destruction without doubt will cause changes. A possible effect will be the decrease in fox numbers. WEBER (1983) assumed that the number of dens can possibly become a limiting factor in areas with unsuitable soil. But more probably, foxes would find other sites certainly closer to houses and that would cause problems to both humans and foxes.

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Zusammenfassung

Kennzeichen und Verteilung von Aufzuchtbauen beim Rotfuchs (Vulpes vulpes) in einem gebirgigen Habitat

Fuchsbaue wurden seit 1986 in einem 30 km^2 großen Gebiet des Schweizer Jura gesucht und überwacht. Im Jahre 1990 wurden Lage und Verteilung der Baue untersucht, um Aufzuchtbaue mit den übrigen, anderweitig genutzten Bauen vergleichen zu können. Es wurden 62 Baue gefunden (0,33/km^2). Die Aufzuchtbaue machen 19,4 % der Gesamtzahl vorhandener Baue aus (1,88/km^2). Ein Vergleich der Lage von Aufzuchtbauen mit der anderer Baue zeigt nur eine Besonderheit: die Aufzuchtbaue hatten deutlich mehr Eingänge. Von Menschen geschaffene Strukturen und von Dachsen gegrabene Baue wurden als Aufzuchtbaue genutzt.

Die Aufzuchtbaue waren von Straßen und Häusern nicht weiter entfernt als die übrigen Baue, und sie waren nicht regelmäßig über das Untersuchungsgebiet verteilt. Dieselben Aufzuchtbaue wurden über mehrere Jahre benutzt. Die Benutzung und Verteilung der Aufzuchtbaue waren begrenzt von der Zahl günstig gelegener vorhandener Baue. Die Anzahl der Aufzuchtbaue kann grundsätzlich genutzt werden, um die Anzahl von Füchsen in einem Gebiet abzuschätzen. Dazu muß jedoch die soziale Organisation der betroffenen Population bekannt sein.

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Zur Zytologie eines hochspezialisierten Sebozyten am Beispiel der holokrinen Analbeuteldrüsen der Hauskatze, *Felis silvestris* f. catus

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Abstract

The cytology of a highly specialized sebocyte, as demonstrated in the holocrine glands of anal sacs in the domestic cat, Felis silvestris f. catus

Studied seasonal changes in organell equipment of holocrine glands of anal sacs in the female domestic cat with regard to specific glandular functions in pheromone production. Similar observations from scent marking organs in other mammals are discussed. The cytological dynamics observed are particularly connected with mitochondria and the endoplasmatic reticulum and could be related to lipogenesis.

Einleitung

Bei vielen Säugetiergruppen besitzen speziell die von den Drüsenorganen der Analregion produzierten Sekrete, denen Pheromoneigenschaften zugeschrieben werden (ALBONE 1984), eine große Bedeutung für soziale Interaktionen. Zu nennen sind z. B. das Fortpflanzungs- oder Territorialverhalten (EISENBERG und KLEIMAN 1972), aber auch die Spezies-, Gruppen- und Individualerkennung (MYKYTOWYCZ 1972; STUBBE 1970). Dem Sekret der Analbeutel kann neben den genannten Funktionen auch die Aufgabe als Defensivwaffe (KRUSKA 1988), wie beim Stinktier (*Mephitis mephitis*) und beim Iltis (*Mustela putorius*), zufallen.

Bei der Hauskatze entspricht der Aufbau der Analbeutel und ihrer Drüsen dem typischen Strukturtypus von Markierungsorganen bei Karnivoren als eine Kombination spezialisierter Talg- und Schlauchdrüsen (FLACHSBARTH 1990; GORMAN und TROWBRIDGE 1989; GREER und CALHOUN 1966; KRÖLLING 1927). Beide Drüsentypen geben ihr Sekretionsprodukt über eigene Drüsengänge in die Analbeutelhöhle ab, wo das Mischsekret durch mikrobielle Tätigkeit (ALBONE und EGLINTON 1974) zum reifen Analbeutelsekret modifiziert wird. Dieses kann mittels Kontraktion der den Analbeutel umgebenden Abspaltung des M. sphincter ani externus (MARTIN et al. 1974) willkürlich über den Analbeutelgang, der in der Zona cutanea ani mündet, auf die Körperoberfläche abgegeben werden.

Die holokrinen und die apokrinen Drüsen des Analbeutels der Katze lassen im Jahresverlauf strukturelle Veränderungen erkennen, die dem jahreszeitlichen Reproduktionszyklus dieser Tiere zugeordnet sind. Bei der weiblichen Katze ist zudem in der Gravidität eine charakteristische Strukturänderung der Analbeuteldrüsen zu beobachten (FLACHSBARTH et al. 1992a). In der vorliegenden Arbeit soll ausschließlich über die Ultramorphologie der holokrinen Analbeuteldrüsenzellen weiblicher, unkastrierter, nicht trächtiger Katzen unter besonderer Berücksichtigung ihrer Funktion als hochspezialisierte Sebozyten berichtet werden. Die Morphologie der apokrinen Analbeuteldrüsen wird an anderer Stelle vorgestellt (FLACHSBARTH et al. 1992b).

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Material und Methode

Das Probenmaterial entstammt zu euthanasierenden Patienten oder Versuchstieren tierärztlicher Einrichtungen. Es sind sieben unkastrierte, nicht trächtige weibliche Katzen aus den Monaten Januar, Februar, April, Mai, August, Oktober und Dezember untersucht worden.

Die unmittelbar nach Eintritt des Todes exstirpierten Analbeutel wurden für die elektronenmikroskopische Präparation in einem Gemisch nach KARNOVSKY (1965) bei 4 °C für mindestens 24 h fixiert, in 1%iger Osmiumtetroxidlösung nachfixiert, über Ethanol dehydriert und in Epon 812 (Serva) eingebettet. Die lichtmikroskopische Vororientierung erfolgte an mit Toluidin-Blau gefärbten 0,5 bis 1,0 µm dicken Semidünnschnitten; die 60 bis 100 nm dicken Ultradünnschnitte wurden mit Uranylazetat und Bleizitrat (VENABLE und COGGESHALL 1965) kontrastiert und mit einem Zeiss EM 10 bei 60 kV ausgewertet.

Für den allgemeinen Nachweis von Lipiden wurden von in 4%igem neutralem Formalin mit 2,5%igem Kalziumzusatz (LILLIE und FULLMER 1976) bei 4 °C für mindestens 24 h fixierten Proben Kryostatschnitte hergestellt. Ihre Färbung erfolgte mit gesättigter Sudan-Schwarz-B-Lösung in 70%igem Ethanol bei 4 °C nach BARKA und ANDERSON (1963) mit Kontrollen an azetonbehandeltem Material. Zum Nachweis von Phospholipiden und Cholesterol wurde zusätzlich eine vorausgehende lipidstabilisierende Bromierung durch Inkubation in 2,5%igem wäßrigen Brom und Spülung mit 0,5%igem Natriumdisulfit (BAYLISS-HIGH 1981), ebenfalls mit Kontrollen an azetonbehandeltem Material, vorgenommen.

Ergebnisse

Bei den holokrinen Analbeuteldrüsen handelt es sich um zusammengesetzte verzweigt-azinöse Drüsen, deren Azini periphere Rand- und zentrale Binnenzellen enthalten. Aufgrund der morphologisch erkennbaren Sekretionsaktivität sowie von Vorgängen des Drüsenauf- und -abbaues können die holokrinen Drüsen den Stadien der ansteigenden Sekretion im Frühjahr, der Hauptsekretion mit je einem Sekretionsmaximum im Früh- und Spätsommer und der abklingenden Sekretion im Herbst und Winter zugeordnet werden.

Die Drüsenmorphologie im Stadium der ansteigenden Sekretion und im Übergang zum Stadium der Hauptsekretion

Der Drüsenaufbau im Frühjahr nimmt seinen Ausgang von den Basalzellen des Drüsengangepithels, die Zellknospen (Abb. 1), als Vorläufer der Drüsenazini, in das grundsubstanzreiche interstitielle Bindegewebe vorschieben. Die so entstandenen Zellen besitzen anfangs nur ein saumartiges Zytoplasma mit zarten, gegen die Basalmembran gerichteten Ausläufern (Abb. 2). Die zunächst stark aufgefaltete Zellmembran glättet sich mit zunehmender Zellgröße und bildet gegenüber der Basalmembran Hemidesmosomen, zu den Nachbarzellen Desmosomen aus. Massive Filamentbündel verlaufen parallel zum Kern; mit zunehmendem Zellwachstum verteilen sie sich als zarte Fädchen über das ganze Zytoplasma. Dieses ist reich an Glykogenschollen sowie Ribosomen; sekretorisch bedeutsame Organellen wie glattes und rauhes Endoplasmatisches Retikulum (ER) oder der Golgiapparat sind nur spärlich ausgeprägt. Entsprechend sind auch osmiophile Sekretgranula nur selten zu finden. Ihr hoher Lipidgehalt ist durch eine intensive Schwärzung nach Sudan-Schwarz-B-Färbung deutlich nachweisbar; mit vorausgehender Bromierung erhöht sich ihre Anfärbbarkeit noch. Die polymorphen Mitochondrien lassen sich dem Crista-Typ zuordnen (Abb. 2). Die Zellkerne sind euchromatinreich mit einem oft randständigen oder doppelten Nukleolus; z. T. lassen sich Mitosefiguren beobachten.

Zur Sekretproduktion übergehende Zellen kennzeichnet eine veränderte Organellenausstattung. Rauhes ER ist als lokal geringfügig dilatiertes, weit verzweigtes Netzwerk anzutreffen. Es bildet zudem aus vielen konzentrisch gelagerten Röhren wirbelartige Strukturen (Abb. 3) aus. Kleine Gebilde dieser Art weisen zentral zahlreiche Ribosomen auf, die aber auch im übrigen Zytoplasma neben Polyribosomen in großen Mengen zu

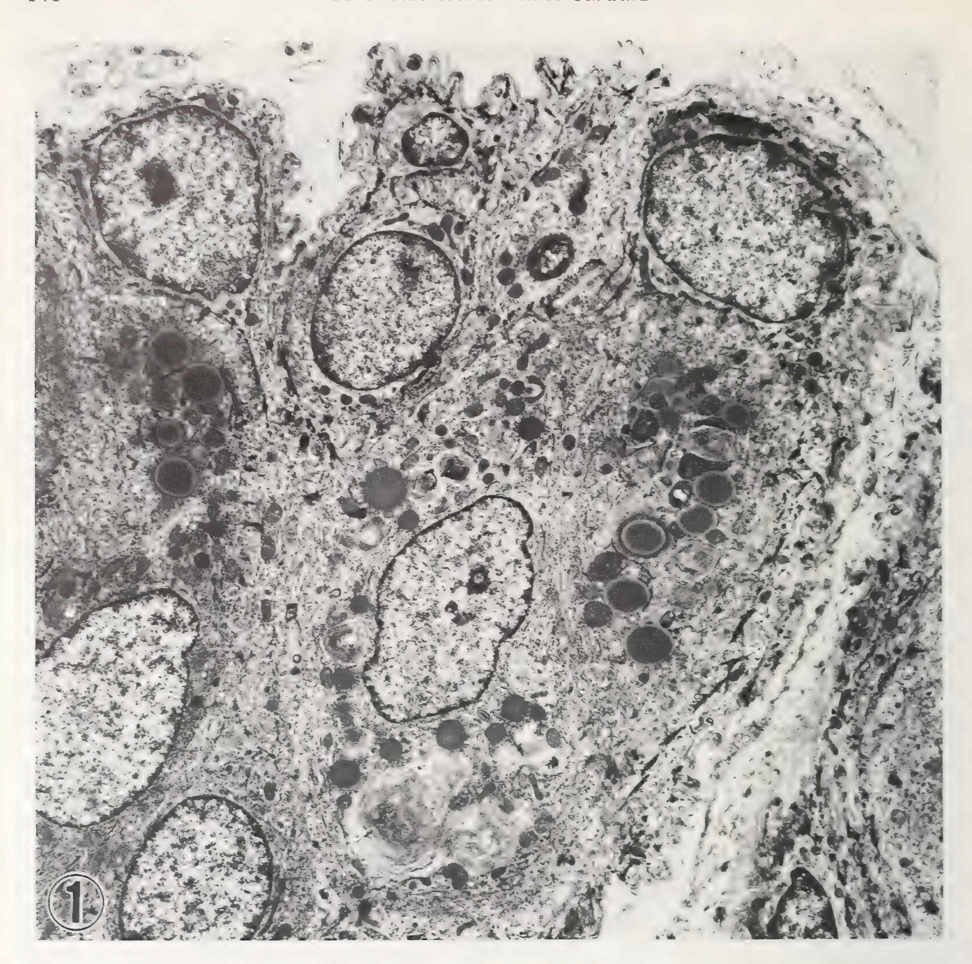


Abb. 1. Ausbildung von Zellknospen im Stadium der ansteigenden Sekretion (Vergrößerung 4000fach)

finden sind. Einige Wirbelformationen sind kombiniert aus rauhem und glattem ER aufgebaut; vorwiegend aus glattem ER bestehende Strukturen können ein vesikelartig gekammertes Zentrum aufweisen (Abb. 3). Die Masse dieser Organelle verteilt sich jedoch in Form von Vesikeln, die strukturell denen des wohl ausgebildeten Golgiapparates gleichen, über das gesamte Zytoplasma. Die zahlreichen, polymorphen Mitochondrien haben eine sehr dichte Matrix, die eine sichere Klassifizierung in Crista- oder Tubulustyp nicht immer zuläßt (Abb. 4); das Auftreten des letzteren häuft sich jedoch bei zunehmendem Gehalt der Zellen an Sekretgranula. Diese erreichen zunächst die halbe bis dreifache Größe der Mitochondrien, zu denen sie oft eine enge Lagebeziehung zeigen. Die Mitochondrien schmiegen sich halbmondförmig und z. T. in diese übergehend um die Lipidtröpfchen (Abb. 5). Einige von ihnen scheinen von einer membranähnlichen Abgrenzung umgeben zu sein (Abb. 5): ein Eindruck, der durch das sternförmig auf sie zulaufende und um sie einen feinkörnigen Kranz bildende rauhe ER (Abb. 4) unterstützt wird. Die Sekretgranula können, als vermutlich eine Möglichkeit ihres Wachstums, konfluieren, jedoch nicht unkontrolliert. Prall mit Sekretionsprodukt gefüllte Zellen schmelzen im Sinne holokriner Sekretion ein.

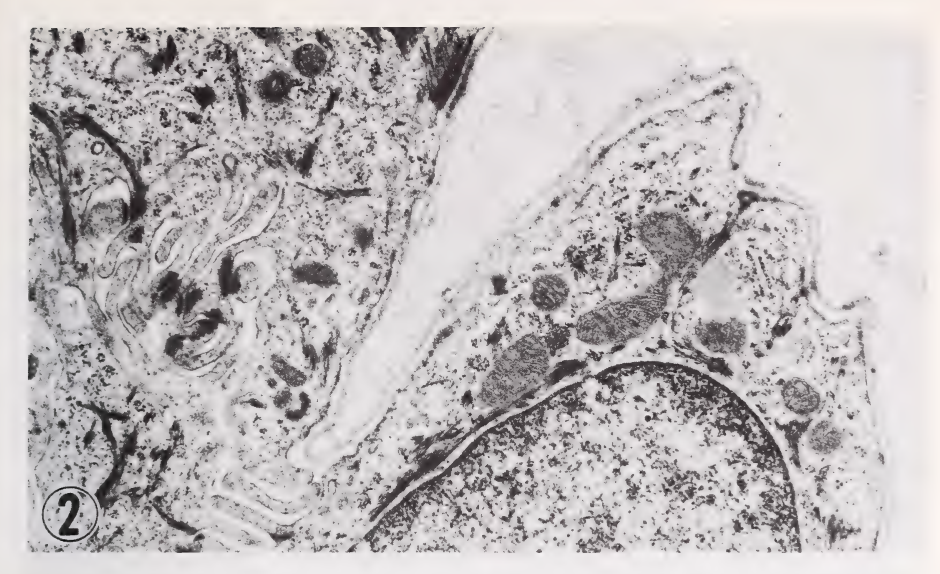


Abb. 2. Randzelle einer Zellknospe mit Mitochondrien vom Crista-Typ (Vergrößerung 18 000fach)

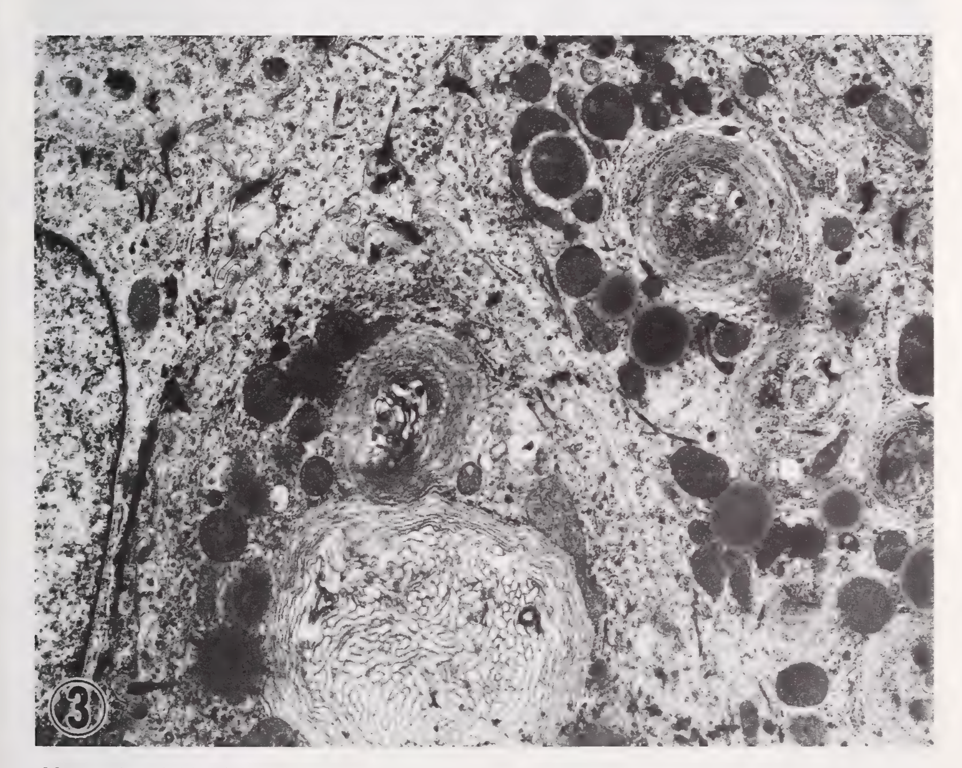


Abb. 3. Sekret bildende Drüsenzellen im Stadium der ansteigenden Sekretion mit spiralig angeordnetem ER (Vergrößerung 10 000fach)

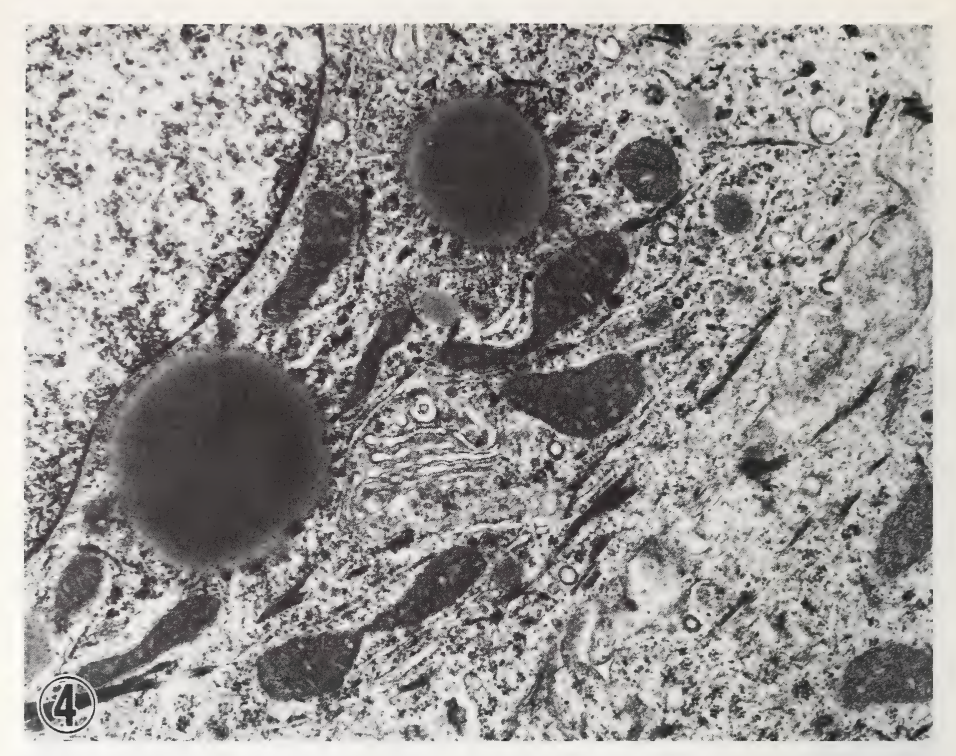


Abb. 4. Sekret bildende Drüsenzelle im Stadium der ansteigenden Sekretion mit sternförmig auf die Sekretgranula zulaufendem rauhen ER und nicht eindeutig typisierbaren Mitochondrien (Vergrößerung 19 500fach)

Die Drüsenmorphologie im Stadium der Hauptsekretion und im Übergang zum Stadium der abklingenden Sekretion

Bei Erreichen des ersten Sekretionsmaximums zeigt sich wiederum eine Modifikation der Ultrastruktur des Drüsenepithels. Das Zytoplasma der Drüsenzellen wird auch elektronenoptisch undurchdringlich dicht; nur wie ins Zytoplasma eingestreut wirkende Desmosomen markieren den Verlauf der Zellgrenzen. Sekretorisch bedeutsame Organellen sind drastisch reduziert, vom rauhen ER sind nur noch einige kurze Abschnitte erkennbar. Die Größe der Sekretgranula hat auf das zehn- bis zwanzigfache der durchschnittlichen Mitochondriengröße zugenommen. Die sehr dichte Matrix der zahlreichen, polymorphen Mitochondrien erschwert ihre Typisierung; es überwiegen jedoch Tubuli. In der Nähe von Lipidtröpfchen scheinen die Mitochondrien zu kondensieren, sie werden kleiner und dichter und besitzen z. T. osmiophile Einschlüsse.

Im Spätsommer zeigen die holokrinen Analbeuteldrüsen neben einem zweiten, kleineren Sekretionspeak auch Anzeichen der Drüsenrückbildung, was sich in ihrer Zytologie dokumentiert. Die Zellen weisen eine von der Azinusperipherie zum Zentrum hin deutlich zunehmende Dichte ihres Zytoplasmas auf (Abb. 6), die solche mit dichtem, weniger dichtem und transparentem Zytoplasma unterscheidbar macht und mit dem Differenzierungsgrad der Zellen positiv korreliert ist. Die unterschiedlichen Zytoplasmadichten lassen die Zellkonturen deutlich erkennbar werden. In den zentral gelegenen Binnenzellen entsprechen rauhes und glattes ER sowie der Golgiapparat der im Frühjahr beschriebenen Situation, nur ihre Ausprägung ist geringer. In den Zellen mit weniger dichtem Zyto-

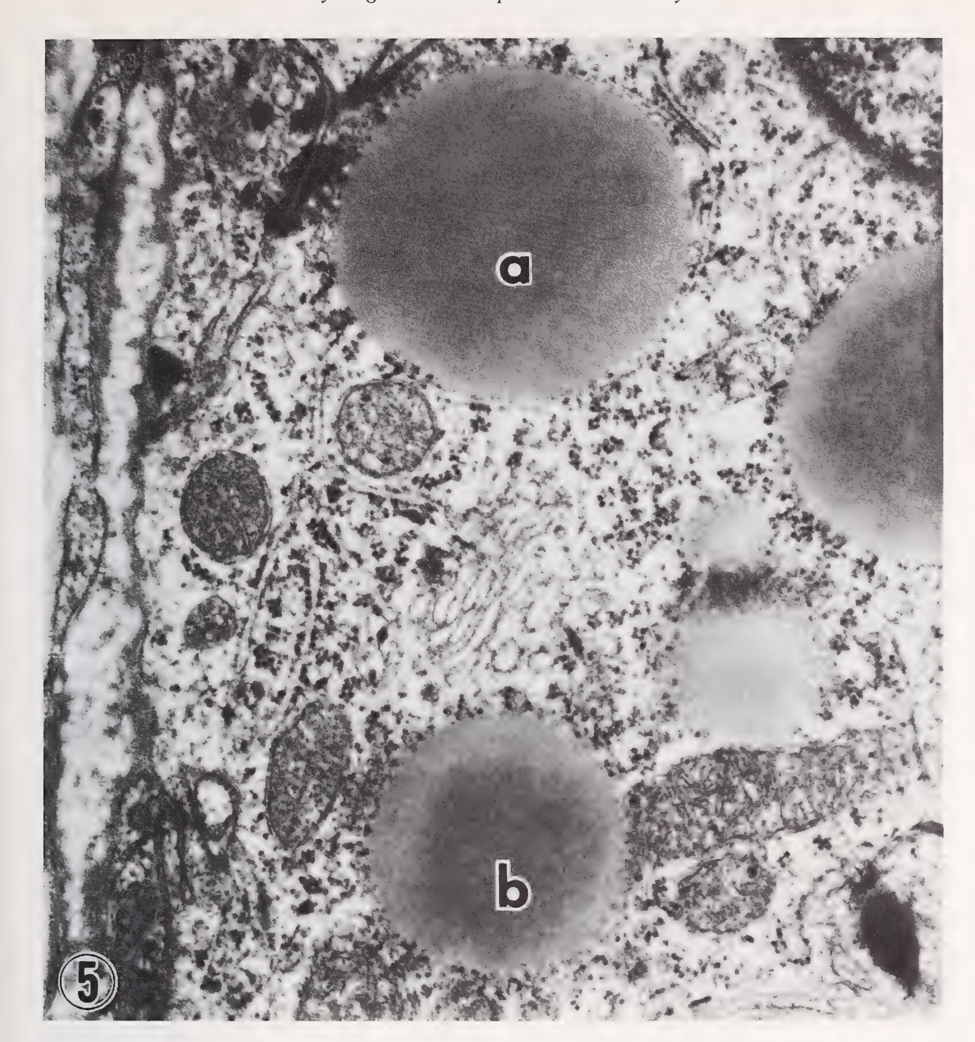


Abb. 5. a-Lipidtröpfchen von Doppelmembranen des ER zirkulär umgeben; b-Lipidtröpfchen sternförmig von rauhem ER umgeben und in unmittelbarer Nähe zu einem Mitochondrium vom Tubulustyp (Vergrößerung 62 500fach)

plasma besitzen die wirbelartigen Strukturen z.T. keine Membransysteme (Abb. 7), sondern zeichnen sich als konzentrische Anordnungen von Ribosomen ab, die auch im übrigen Zytoplasma zahlreich vertreten sind. In den Azinusrandzellen finden sich nur vereinzelt längere Schläuche des rauhen und kurze Tubuli des glatten ER sowie einige Strukturen des Golgisystems. Die von diesen Organellen abstammenden und nur in den zentralen Zellen noch häufiger auftretenden Vesikel sind vermehrt mit feingranulärem Inhalt gefüllt. Die Mitochondrien weisen in den Zentralzellen sowohl Cristae als auch Tubuli auf; Azinusrandzellen besitzen ausschließlich Mitochondrien vom Crista-Typ. Unregelmäßig konfluierende, mit einer wenig elektronendichten Substanz gefüllte Räume, in denen kondensierte Membrananteile liegen können, fallen häufiger in den zentralen Zellen auf (Abb. 6). Diese besitzen auch die meisten Sekretgranula, die jedoch im Vergleich zum ersten Sekretionsmaximum in Anzahl und Größe deutlich abgenommen haben.

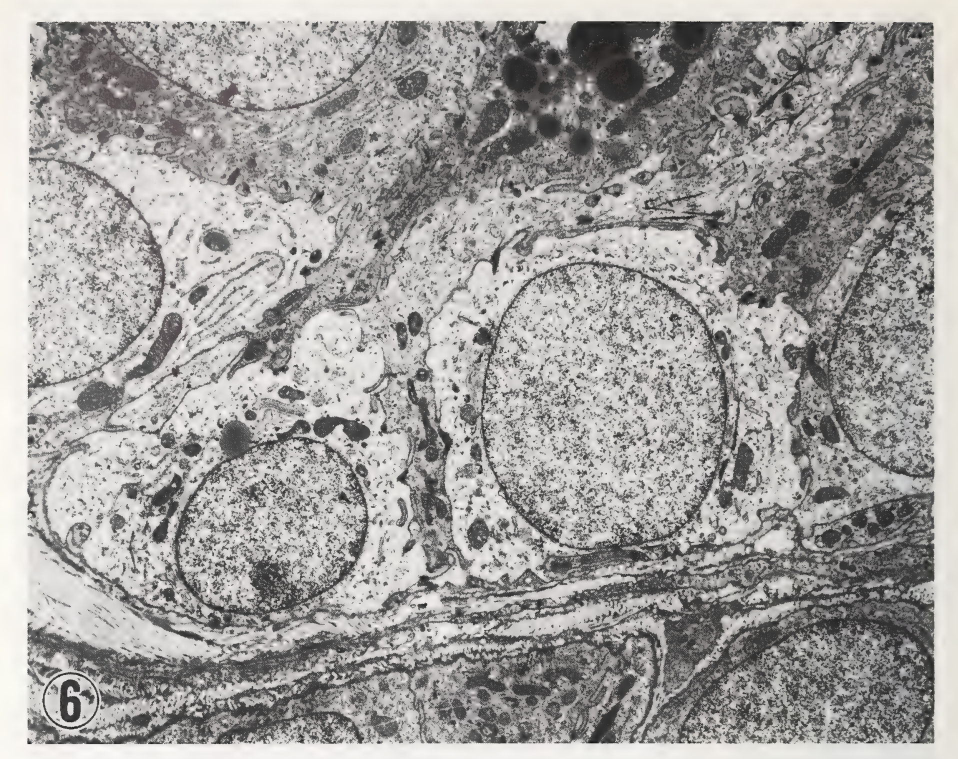


Abb. 6. Drüsenazinus im Stadium der abklingenden Sekretion, von peripher nach zentral zunehmende Dichte des Zytoplasmas (Vergrößerung 5000fach)

Letztgenannte Charakteristika der Sekretgranula nehmen in den peripheren Azinuszellen stark ab; die Randzellen zeigen nur sehr selten kleine Sekretgranula. Einige dieser Zellen scheinen zu verdämmern: ihr Zytoplasma wird durchscheinend, der Kern schrumpft und bekommt eine ungleichmäßige Kontur und die Zellen verschwinden, ohne daß ein holokriner Einschmelzungsprozeß oder eine Nekrose beobachtet werden könnte.

Diskussion

Die Zellen der holokrinen Analbeuteldrüse der Katze sind als hochaktive, spezialisierte Sebozyten anzusprechen. Ihre Zytologie erfährt unter dem Einfluß des Zeitpunktes der Probennahme und des Reproduktionsstatus des untersuchten Tieres große Änderungen, die das unterschiedliche und aus ihrer Funktion als Pheromonproduzenten (Albone 1984) bedingte Aktivitätsniveau widerspiegeln.

Ihre konstante Ausstattung mit reichlich Ribosomen und Polyribosomen gewährleistet zu jedem Zeitpunkt die Versorgung der hochaktiven Zellen mit zellintern verbleibenden Substanzen, z. B. Enzymen.

Beispielhaft für die funktionell bedingten Änderungen der Morphologie sind die Mitochondrien zu nennen. In den Basalzellen des Drüsengangepithels sowie in aus diesen hervorgegangenen jungen Azini sind vielgestaltige Mitochondrien vom Crista-Typ vorhanden. Mit Einsetzen der Sekretproduktion zeigen die Mitochondrien eine verdichtete Matrix und zunehmendes Auftreten tubulärer Innenstrukturen. Eine eindeutige Typisierung ist deshalb, ebenso wie bei den von Kayanja und Schliemann (1981) für die

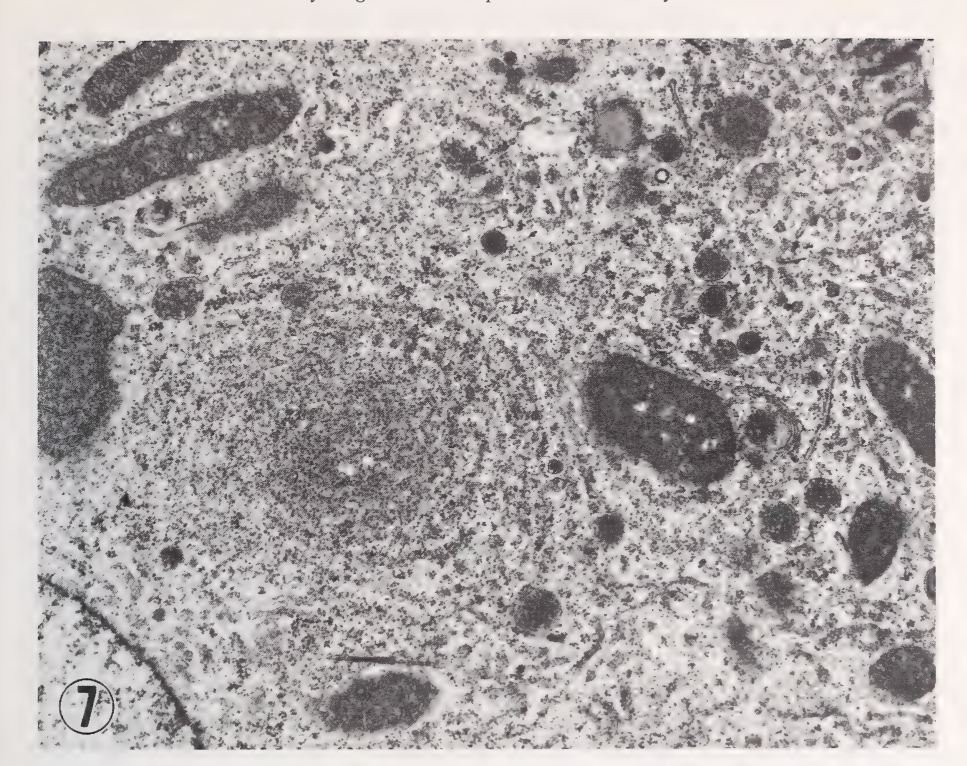


Abb. 7. Ausschnitt einer zentralen Drüsenzelle im Stadium der abklingenden Sekretion mit wirbelartig gelagerten Ribosomen, Mitochondrien nicht eindeutig typisierbar (Vergrößerung 10 000fach)

holokrinen Analbeuteldrüsen der Großfleck-Ginsterkatze (*Genetta tigrina*) beschriebenen Befunde, nicht mehr möglich. Die Mitochondrien vom Tubulus-Typ, die zur Zeit des ersten Sekretionsmaximums am zahlreichsten vorhanden sind, mögen auf eine Beteiligung dieser Zellen am Steroidstoffwechsel hinweisen (Ghadially 1988). Die Produktion von Steroidderivaten, die als mögliche Pheromone diskutiert werden (Albone 1977), verläuft demnach weitgehend parallel zum disaisonalen Fortpflanzungszyklus der Hauskatze (Strauss 1986).

Auch die direkt an der Sekretbereitung beteiligten Organellen wie glattes und rauhes ER und der Golgiapparat zeigen ihre größte Ausprägung und Aktivität im späten Frühjahr bzw. Frühsommer. Das ER liegt, wie auch von Kayanja und Schliemann (1981) für die holokrinen Analbeuteldrüsen der Gloßfleck-Ginsterkatze (*Genetta tigrina*) beschrieben, in wirbelartiger Anordnung vor, die von anderen Autoren (Gasse und Peukert-Adam 1985; Ghadially 1988) in unterschiedlichen, hochaktiven Zellen als Aktivitätshypertrophie interpretiert wird.

Primäre Lysosomen konnten aufgrund ihrer unscheinbaren Morphologie nicht aus der Gruppe der Vesikel-Strukturen differenziert werden. Die Notwendigkeit ihres Vorhandenseins für die Zytolyse im Rahmen der holokrinen Sekretion wird jedoch von Brandes und Bertini (1965) hervorgehoben. Peroxisomen, die in modifizierten Talgdrüsenorganen regelmäßig gezeigt werden konnten (Gorgas und Völkl 1984; Gorgas und Zaar 1984; Zaar und Gorgas 1985), ließen sich hier ohne histochemische Untersuchungstechniken ebenfalls nicht darstellen.

Das vornehmliche Sekretionsprodukt der holokrinen Analbeuteldrüsen stellt sich in Form der beschriebenen Sekretgranula dar. Mittels der Sudan-Schwarz-B-Färbung läßt

sich ihr hoher Lipidgehalt nachweisen; eine Intensivierung der Anfärbbarkeit nach einer Behandlung mit Brom spricht für das Vorkommen von Cholesterolabkömmlingen (Bayliss-High 1981). Die genaue Lokalisation der Lipogenese in der Zelle ist umstritten und steht in unmittelbarem Zusammenhang mit der Frage nach einer das fettige Zellprodukt umgebenden Membran. Kleinig und Sitte (1986) bezeichnen Fetttröpfchen, die am ER entstehen und sich mit einer elektronendichten Schicht amphiphiler Moleküle, einer half-unit-membrane, umgeben, als Oleosomen. Jenkinson et al. (1985) zeigen in Hauttalgdrüsen das Entstehen von Fettsubstanzen am glatten ER, das Fetttröpfchen hufeisenförmig umgeben und so eine Membran vortäuschen kann. Für Niizuma (1981) entstehen membranumgebene Lipide im Golgiapparat reifender Zellen in menschlichen Talgdrüsen. Unter Beteiligung des glatten ER konfluieren die Tröpfchen, die ursprüngliche Membran geht verloren. Lipogenese durch mitochondriale Enzyme und nachfolgende Umwandlung von Mitochondrien in Fetttröpfchen wird von Jenkinson et al. (1979) in apokrinen Hautdrüsen von Rindern, von Ghadially (1988) im Herzmuskel des Rindes und von Atoji et al. (1989a) in der Präputialdrüse des japanischen Seraus (*Capricornis crispus*) beschrieben. In den Infraorbitaldrüsen derselben Tierart wird die Lipogenese den Mitochondrien sowie dem glatten und rauhen ER zugeordnet (Atoji et al. 1989b). In den holokrinen Analbeuteldrüsen der Hauskatze scheinen einige Lipidgranula frei im Zytoplasma zu liegen; andere, besonders in unmittelbarer Nähe von Mitochondrien oder des rauhen ER, sind scheinbar von einer Membran umgeben. Es ist denkbar, daß Fettsubstanzen alternativ von verschiedenen Organellen erstellt werden können. Die holokrinen Analbeuteldrüsen der Katze, besonders im Stadium der ansteigenden Sekretion, könnten sich daher für weitere Untersuchungen zur Lipogenese anbieten.

Die Zellkerne der Drüsenzellen imponieren durch ihren Euchromatinreichtum, der in Verbindung mit den ausgeprägten Nucleoli für große Kernaktivität spricht. Die Lokalisation der Kernkörperchen am Kernrand ist nach Ghadially (1988) ebenfalls als Aktivitätsmerkmal zu werten. Der hohe Euchromatingehalt unterscheidet diese holokrinen Zellen von den Talgdrüsenzellen der allgemeinen Körperdecke, deren Kerne einen größeren Anteil von Heterochromatin aufweisen (Jenkinson et al. 1985).

Die Hauskatze (*Felis silvestris* f. catus) zeigt im Vergleich zu ihrer Stammform, der Falbkatze (*Felis silvestris libica*), eine für die Haustiere typische Steigerung der Fertilität (Haase 1985; Herre und Röhrs 1990) mit einem zweiten Fortpflanzungszeitraum im Spätsommer (Strauss 1986). Zu diesem parallel verläuft ein zweites Sekretionsmaximum der holokrinen Analbeuteldrüsen, allerdings wesentlich moderater als das erste (Flachsbarth 1990). Während die Tubulusstruktur der Mitochondrien der zentralen Binnenzellen auch eine forcierte Sekretionsaktivität von Cholesterolabkömmlingen vermuten läßt, so weist der Crista-Typ der Mitochondrien in den zum Azinusrand orientierten Binnenzellen sowie den Randzellen auf eine verzögerte oder ausbleibende Zelldifferenzierung und herabgesetzte Sekretionstätigkeit hin. Auch die kleiner bleibenden Wirbelstrukturen des ER bzw. die fehlende Ausbildung von Tubulusstrukturen in ihnen sowie die herabgesetzte Anzahl von Golgikomplexen deuten auf eine verminderte Zellaktivität hin. Insgesamt lassen das teilweise Ausbleiben der Zelldifferenzierung bzw. das Verdämmern der Randzellen eine drastische Reduzierung der Sekretionstätigkeit erkennen.

Die holokrinen Analbeuteldrüsen der Hauskatze zeigen somit Charakteristika, die in verschiedenster Kombination als typische Eigenschaften bei Markierungsorganen von Säugetieren gefunden werden können: Sie weisen eine deutliche Saisonalität auf, die sich an den Zeiten sexueller Aktivität der Tiere orientiert (Baker 1988; Johnson 1973). Ihre Sekretionsintensität wird außerdem durch Reproduktionsstatus und Geschlecht maßgeblich beeinflußt (Flachsbarth 1990; Johnston 1983; Kodera et al. 1982; Starck und Poduschka 1982). Der sekretionsfördernde Einfluß von Androgenen auf Talgdrüsen ist dabei unbestritten (Ebling 1974; Luderschmidt 1985). Die Beteiligung weiblicher Geschlechtshormone an der Steuerung modifizierter Sebozyten in hochspezialisierten

Duftdrüsenorganen wird jedoch diskutiert (Atoji et al. 1989a; Heymann et al. 1989; Kodera et al. 1982). Die holokrinen Analbeuteldrüsen der Katze sind nach unseren Untersuchungen – anders als von Becker (1991) dargestellt – nicht als ausschließlich androgengesteuerte Drüsen anzusprechen.

Das Sekretionsprodukt der holokrinen Analbeuteldrüsen wird durch das der apokrinen Drüsen und die abschilfernden Massen des Analbeutelepithels zum vollständigen Mischsekret kompletiert (Albone 1984). Dabei dürfte die stark fetthaltige Komponente der holokrinen Drüsen für eine recht lange Haftdauer des zur territorialen Markierung genutzten Sekretes sorgen, während die leichter flüchtige Komponente aus den apokrinen Drüsen eine Kurzzeitinformation liefert, die über die Luft schnell im Umkreis verteilt wird (Gorman und Trowbridge 1989). Die dem Analbeutel eigene Mikroflora und -fauna mag über ihre spezielle Zusammensetzung Individuen (Gorman et al. 1974) oder zumindest Angehörige verschiedener Tiergruppen (Mykytowycz 1970) voneinander unterscheidbar machen.

Zusammenfassung

Die sich saisonal ändernde Organellenausstattung der Sebozyten holokriner Analbeuteldrüsen von weiblichen Hauskatzen wird aufgezeigt und im Hinblick auf die Funktion dieser Drüsen als Pheromonproduzenten diskutiert. Dabei wird auf parallele Erscheinungen bei diversen Markierungsorganen von Säugetieren hingewiesen. Die der zytologischen Dynamik besonders stark unterworfenen Organellen (Mitochondrien und Endoplasmatisches Retikulum) werden hinsichtlich ihrer Bedeutung für die Lipogenese hinterfragt.

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Cytogenetics and karyosystematics of phyllotine rodents (Cricetidae, Sigmodontinae)

III. New data on the distribution and variability of karyomorphs of the genus *Eligmodontia*

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Abstract

Studied bone-marrow banded and Ag-NORs karyotypes of the South American phyllotine *Eligmodontia* in three populations of northern Patagonia (Argentina): south of Nahuel Huapi Lake and Los Menucos (Rio Negro Province), and Junín de los Andes (Neuquén Province). In the first locality, two polymorphic variants (2n = 34 and 2n = 32) were found; in the other two localities the 2n = 44 karyomorph previously reported as belonging to *Eligmodontia typus,* was dominant, but it was found in sympatry with two polymorphic variants (2n = 33–34) corresponding to the Nahuel Huapi karyotype, thus confirming that these karyomorphs belong to different, probably synmorphic species. The 2n = 34 variant was found for the first time in the Nahuel Huapi and in Junín de los Andes populations. G-banding and Ag-NORs proved that 2n = 44 and the polymorphic variants 2n = 32-33-34 karyomorphs are strikingly different, thus confirming a full species status for each of them.

Introduction

The desertic long-tailed phyllotine mice of the genus *Eligmodontia* are widely distributed in the southern cone of South America, from south of Perú to Tierra del Fuego. Several species have been named (according to review in Tate 1932), but after Hershkovitz's revision (1962), it was currently considered that the genus comprises only one species with two subspecies: *E. typus typus* and *E. typus puerulus* (Cabrera 1961; Honacki et al. 1982). However, in a recent paper on the karyosystematics of several Argentinian populations (Ortells et al. 1989), three different allopatric karyomorphs (2n = 44, 2n = 32-33 and 2n = 50) have been reported, stressing the view that *Eligmodontia* is a polytypic genus. The 2n = 44 form was ascribed to the type species *E. typus,* and that of 2n = 50 (previously described by Pearson and Patton 1976) to *E. typus puerulus,* whereas the polymorphic 2n = 32-33 form was of no definite identification, being assigned to *Eligmodontia* sp.

New and recent collecting in northern Patagonia allowed us to gain new knowledge on the distribution of 2n = 44 and 2n = 32-33 chromosomal species, finding that the two karyomorphs occur in sympatry, and that they are strikingly different in the Ag-NOR and in G-banding pattern. It also allowed us to find the so far unknown 2n = 34 variant of the polymorphic form, and to study the meiotic behavior of the heterozygous 2n = 33 variant.

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Material and methods

Thirty-one animals from three different localities in northern Patagonia (Argentina) have been processed in this study. Two females were obtained by OLIVER PEARSON (University of California, Berkeley) in the steppe biome 13 km south of Nahuel Huapi Lake (Rio Negro Province, Fig. 1). Four females and nine males were caught by ALLAN DICKERMAN (University of Wisconsin) and ADRIAN MONJEAU (University of Comahue, San Carlos de Bariloche), 15 km S.E. of Los Menucos (Rio Negro Province). Ten females and six males were collected at Estancia Quenquetrén, 110 km southeast of Junín de los Andes (Neuquén Province) by ANDRÉS NOVARO and ANGEL CAPURRO (University of Buenos Aires). Animals were captured in the field with Sherman live traps and processed in the laboratory.

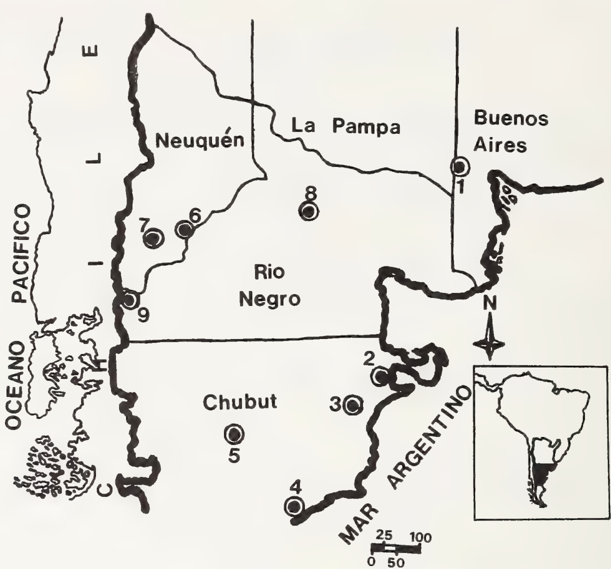


Fig. 1. Map showing where samples of *Eligmodontia* were collected and localities. 1 = Chasicó, 2 = Puerto Madryn, 3 = 28 de Julio, 4 = Pampa Salamanca, 5 = Paso de Indios, 6 = Los Lagos, 7 = Junín de los Andes, 8 = Los Menucos, 9 = Nahuel Huapi

Bone-marrow metaphases were obtained following a modified technique of ROTHFELS and SIMINOVICH (1958). Testicular material was treated according to some modifications of EVANS et al. (1964). Some specimens were also previously treated with yeast following LEE and ELDER (1980). Ag-NOR identification was performed according to HOWELL and BLACK (1980). Buffered Giemsa stain at 10 % was used to stain mitotic and meiotic preparations, but a 3 % concentration was used in Ag-NORs staining. G- and C-banding was obtained in a few specimens following SEABRIGHT (1971) and SUMNER (1972), respectively. Voucher specimens were deposited in the collection of mammals at the Municipal Museum of Natural History of Mar del Plata and the Museum of Zoology, University of Michigan. Chromosomal lengths were expressed as a percentage of the female haploid set (FHS) and calculated from a minimum of 10 metaphases. Chromosome size classes followed REIG and KIBLISKY (1969), calling "large" those chromosomes > 9 FSH, "medium-sized" those between 9 and 5.5 FHS, "small" those between 5.5 and 2 FHS and "minute" those < 2 FHS. Chromosome nomenclature according to centromere position followed LEVAN et a!. (1964). FNa values are autosomal arm numbers.

Results

Fifteen animals from Junín de los Andes and twelve from Los Menucos showed equally the 2n = 44, FNa = 44 karyotype. A male from Los Menucos presented a 2n = 33, FNa = 32 karyotype; a female from Junín de los Andes and a female from Nahuel Huapi showed a 2n = 32, FNa = 32 karyotype. A female from Junín de los Andes and another from Nahuel Huapi had an identical karyotype of 2n = 34, FNa = 32.

The 2n = 44, FNa = 44 karyomorph

Karyotype

This karyotype agrees with that previously described as belonging to *E. typus* (ORTELLS et al. 1989). It comprises one very large pair of metacentric (m) and twenty pairs of acrocentric (t) autosomes gradually decreasing in size. Autosomes of pair one are very large and almost fully metacentric (m); their total length is 2.5 times the length of autosomes of pair 2, and each of their arms is larger than the total size of pair 2 autosomes. The remaining autosomal pairs are distributed according to their size: those of 2 and 3 are large; those of pairs 4, 5 and 6 are medium-sized; those of pairs 7 to 20 are small, whereas those of pair 21 are minute. The XY sexual pair comprises the X chromosome, which is metacentric (m) and has the same size as autosomes of pairs 2 and 3. The Y chromosome is subtelocentric (st) and as small as the autosomes of pair 12.

Ag-NORs localization

In the 2n = 44 karyotype the Ag-NORs are located in two large and three medium-sized acrocentric autosomal pairs and in the 21 pair, the smallest autosome of the complement; this one has a low staining frequency. Although the theoretical value is twelve, in most of the plates we found from 5 to 8 chromosomes with Ag-NORs (Fig. 2a). A high frequency of association was found between two of those elements, and occasionally, between three of them (Fig. 2c).

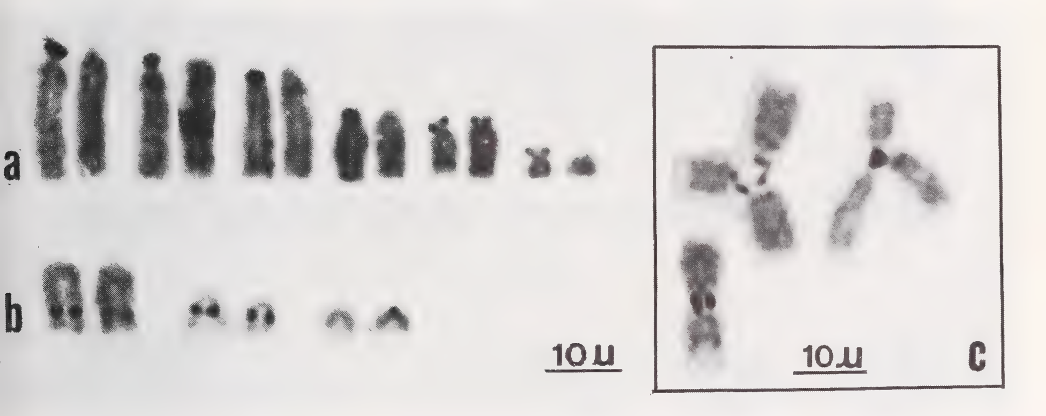


Fig. 2. a: Ag-NOR labeled 2n = 44 karyomorph chromosomes. *b:* NOR association between 2n = 44 karyomorph chromosomes. *c:* Ag-NOR labeled 2n = 33 and 34 karyomorph chromosomes

Complexes of 2n = 32-33-34, FNa = 32

Karyotype 2n = 32

An *Eligmodontia* female from Nahuel Huapi had a 2n = 32 karyotype; it agrees with that of the specimen previously studied as belonging to *Eligmodontia* sp. collected from Los Lagos (Junín de los Andes) (ORTELLS et al. 1989). Pairs 1 to 6 comprise large acrocentric (t) autosomes; pair 7 is made of medium-sized metacentric (m) autosomes, and pairs 8 to 15 are acrocentric (t) chromosomes, decreasing gradually in size from medium to small. The fundamental autosomal number (FNa) is 32. The X chromosomes are of medium size and acrocentric (t) similar to the autosomes of pair 8.

Karyotype 2n = 33

A male from Los Menucos showed a 2n = 33 karyotype, in which the sexual and fifteen autosomal pairs were acrocentric (t), plus an odd metacentric (m) autosome. The fundamental number is FNa = 32 (Ortells et al. 1989). Autosomes of pairs 1 to 6 are large, decreasing gradually in size; the seventh position is occupied by the odd medium-sized metacentric (m); pairs 8 to 15 decrease gradually in size from medium to small. There is an evident size gap between the first six pairs and the remaining set of autosomes. The X chromosome is medium-sized and acrocentric (t) similar to autosomes of pair 8; the Y chromosome is comparable to chromosomes of pair 14. We have been unsuccessful in obtaining good C- and G-banding in this specimen. Pairs 4 and 9 have prominent secondary constrictions located in a medial position, but in pair 4 they are closer to the telomeric end, whereas in pair 9 they are closer to the centromere.

Karyotype 2n = 34

A female from Estancia Quenquetrén and another one from Nahuel Huapi presented a 2n = 34 karyotype in which all 34 elements are acrocentric (t) keeping the FNa of 32. Comparing the 2n = 32 and 33 karyomorphs with that of 2n = 34, the latter does not present a medium-sized metacentric (m) autosome, but instead one additional small acrocentric autosomic pair (Fig. 3).

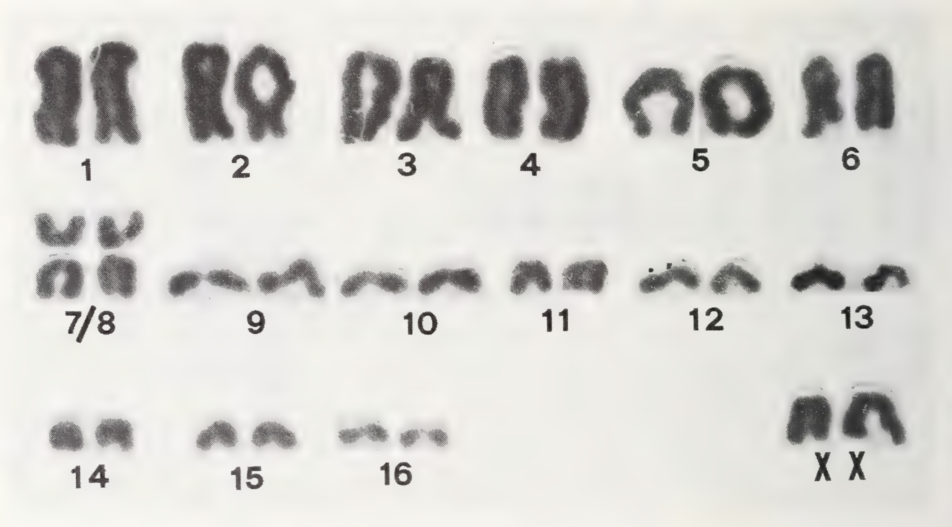


Fig. 3. Bone marrow standard Giemsa staining karyotype of *Eligmodontia* sp. from Estancia Quenquetrén (Junín de los Andes), Neuquén Province, Argentina. 2n = 34; FNa = 32

Ag-NORs localization

In the complexes of 2n = 33 and 34, Ag-NORs staining was identical. The rRNA cistrons of pairs 4 and 9 are in the same morphological position as the secondary constriction. One of the pairs from the group 12 to 15 (where all the autosomes have similar size) carries NORs, which are located in a distal pericentromeric position (Fig. 2b). Pair 9 shows the highest frequency and intensity of staining and the two homologues are usually dyed. Pair 4, which presents a lower intensity of silver staining, is usually stained in the two homologues. Silver was fixed only in a few times on the smallest pair and only one homologous showed Ag-NOR.

Meiosis

Meiosis was studied in the 2n = 33 male. In diplotene, diakinesis and metaphase I, fourteen autosomic bivalents and the XY pair with the classic end-to-end association were observed. Moreover, a characteristic autosomic trivalent was found. It was constituted by two acrocentric elements and the metacentric, which corresponds to the odd biarmed chromosome found in somatic cells (Fig. 4). Six bivalents corresponding to the first six pairs of somatic autosomes are noticeable due to their larger size. The largest pairs form two or three chiasmata. Two chiasmata are regularly shown in three large bivalents, and one or two chiasmata occur in two large bivalents. The remaining bivalents show only a bridge.

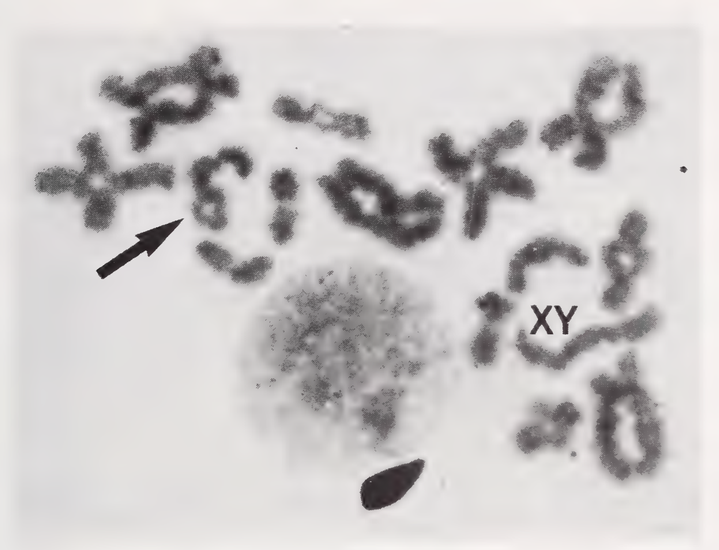


Fig. 4. Diakinesis of the male *Eligmodontia* sp. from Los Menucos, Rio Negro Province, Argentina. 2n = 33; FNa = 32. The arrow points to the trivalent

G- and C-banding

G- and C-bands were obtained in the 2n = 32 and 2n = 34 metaphases from Nahuel Huapi and compared with the 2n = 44 bands previously obtained (Ortells et al. 1989). The two karyomorphs of Nahuel Huapi fully match in arm-to-arm G-bands comparisons, allowing to confirm that metacentric pair 7 of the 2n = 32 karyotype was the result of a Robertsonian fusion of acrocentrics of the 2n = 34 karyotype (Fig. 5a, b).

C-banding of the 2n = 32 karyotype showed pericentromeric positive staining in autosomal pairs 1, 5 to 8 and 11 to 15, as well as in the sex chromosomes. C-banding of 2n = 34 specimen fully matches the pattern found in the 2n = 32 karyotype.

When comparing the 2n = 34 G-bands with those of the 2n = 44 karyotype, few arm-to-arm correspondence was found (Fig. 5c). The metacentric autosomes of the first pair of the 2n = 44 karyotype match the banding pattern of autosomes 2 and 3 of the 2n = 34 karyotype. We found an apparent lack of two bands, one pericentromeric and another telomeric in the long arm of the 2n = 44 metacentric, and another band which is present in the short arm but absent in autosomal pair 3 of the 2n = 34 karyotype. Complete homology was also found in four other autosomal pairs between the two karyotypes (Fig. 5c).

Moreover, regarding the remaining chromosomes, the 2n = 34 karyotype showed 10 autosomes and the X which are not found in the 2n = 44 karyotype, and the latter shows 16 non-shared autosomal pairs.

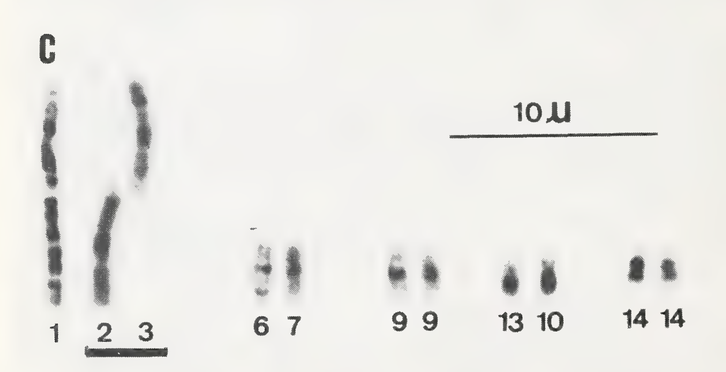


Fig. 5. G-banded karyotypes of *Eligmodontia* sp. from south of Nahuel Huapi Lake, Rio Negro Province, Argentina. *a:* 2n = 32; FNa = 32. *b:* 2n = 34; FNa = 32. *c:* G-banding pattern comparison between *Eligmodontia typus* (left) and *Eligmodontia* sp. (right). The numbers correspond to their position in each species' karyotype

Discussion

The 2n = 44 karyotype found in Los Menucos and Junín de los Andes was identical to the one previously reported from Chasicó (Buenos Aires Province) (Hurtado and Wainberg 1977) and from the same locality and central Chubut Province and referred to as *E. typus* (Ortells et al. 1989). This allows us to extend the distribution of this species 750 km to the west and 800 km to the north of previous chromosomally based records. The 2n = 43 variant found in Chasicó was not found in our new material.

The previously reported 2n = 32-33 karyomorphs from Los Lagos, south of Neuquén Province (Ortells et al. 1989) were found to occur in three new localities: in northern Rio Negro (Nahuel Huapi), south-west of Neuquén (Junín de los Andes) and north-central Rio Negro (Los Menucos), thus confirming the widespread occurrence of this form in northwestern Patagonia. The new samples also allowed to find a 2n = 34 variant of the same polymorphic system which was previously unknown. The study of meiosis of the 2n = 33 heterokaryotype and G-banding comparisons between 2n = 32 and 2n = 34 variants confirmed that all these chromosomal forms belong to one polymorphic system involving a Robertsonian fusion.

The present study also showed a frequent association between two NOR-bearing chromosomes, and an occasional one among three Ag-NOR-marked chromosomes in the 2n = 44 karyotype. This could be related with a tendency toward centric fusions. However, it is evident that it accounts for a part of the chromosomal differences between these two karyomorphs.

The placement of the Ag-NORs in different autosomal pairs and the scarce arm-to-arm homology found between the 2n = 43-44 and the 2n = 32-33-34 karyotypes confirm that a large amount of chromosomal repatterning was involved in the evolution of these two forms, bolstering the previous claim that they belong to two different, albeit probably synmorphic species (Ortells et al. 1989). This conclusion is further confirmed by the finding of sympatry of the two karyomorphs in Los Menucos and Junín de los Andes.

Thus, there is sufficient evidence to confirm that two species of *Eligmodontia* inhabit northern Patagonia. The name to apply to the 2n = 32-33-34 form is still obscure, and this problem must be solved by a thorough taxonomic revision of the entire genus.

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Zusammenfassung

Cytogenetik und Karyosystematik von phyllotinen Rodentia (Cricetidae, Sigmodontinae). III. Neue Daten über Verbreitung und Variabilität von Karyotype der Gattung Eligmodontia

Karyotypen der südamerikanischen Rodentia-Gattung *Eligmodontia* von 3 Populationen aus Nordpatagonien wurden untersucht. Tiere einer Population entstammten der Region südlich des Sees Nahuel Huapi, die einer anderen waren von Los Menucos (Provinz Rio Negro) und die der dritten von Junín de los Andes (Provinz Neuquén). In der ersten Population wurden zwei polymorphe Varianten (2n = 34 und 2n = 32) gefunden. In den beiden anderen war der bislang *Eligmodontia typus* zugeordnete Karyotyp (2n = 44) dominant. Sympatrisch zusätzlich gefunden wurden jedoch auch zwei polymorphe Varianten (2n = 33; 2n = 34), die dem Typus der Nahuel Huapi-Population glichen. Die Variante 2n = 34 wurde erstmalig für die Nahuel Huapi Region und die Population von Junín de los Andes belegt. G-Bandenmuster und vergleichende Untersuchungen am Nucleolus-Organisator nach Dar-

stellung mit Silbernitrat bestätigen, daß die Karyotypen 2n = 44 und die polymorphen Varianten 2n = 32-33-34 auffallend verschieden voneinander sind. Beiden muß sehr wahrscheinlich ein eigener Species-Status zuerkannt werden.

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Burrow structure in the subterranean rodent *Ctenomys talarum*

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Abstract

Analysed the structure of completely excavated burrow systems of Tuco-tuco (*Ctenomys talarum*). Burrow systems of males and females show the same basic design. The main tunnel occupies 48 % of a burrow in total length and is formed by basic units (interfork distances) of 0.9 ± 0.4 m. Subterranean plant biomass was correlated with burrow length and with the number of branches. Soil granulometry affected the diameter and depth of tunnels and soil humidity was correlated with the main tunnel length.

Introduction

South-American caviomorph rodents of the genus *Ctenomys,* called Tuco-tucos are the most numerous in species number of all fossorial rodents (Reig et al. 1990). Tuco-tucos spend most of their lives within plugged burrows, evident by the mounds that result from pushing loosened soil out of the tunnels.

Burrow structure is of main importance in terms of energy costs or burrowing. As a consequence, foraging efficiency and escape from predators are the ultimate factors shaping burrowing behavior (Andersen 1988). Thus, burrows of different mammalian taxa have evolved into broadly convergent structures.

Studies on burrow architecture of North American geomyd rodents suggest that subterranean rodents maximize the energy expended per meter of burrow (Vleck 1981) and that architecture of burrow systems is not adaptive to resource availability (Cameron et al. 1988). Reichman et al. (1982) reported that total length of the burrow and the average number of branches are inversely related to plant productivity. Furthermore, these authors suggest that any spacing rule involves basic building units of the burrow system. This unit can be combined in such a way as to increase overall burrow length in response to resource availability.

The literature contains little information concerning the structure of Tuco-tuco burrow systems, although numerous studies have centered on those of the northern pocket-gopher. For a review on subterranean burrow structures, see Hickman (1990).

The present report offers information based on field observations on the structure of completely excavated burrow systems of the Tuco-tuco, *Ctenomys talarum,* and relates the major features of the burrow with characteristics of the surrounding habitat.

Material and methods

This study was conducted from January to December 1989 at the sandy dune belt from Mar del Cobo (Pdo. Mar Chiquita, Prov. Buenos Aires). Plastic live traps were set at fresh surface mounds. Weight and sex of the Tuco-tuco trapped were recorded. Burrow systems were excavated with a shovel. Tunnels, chambers and mounds were mapped on graph paper. The length of all tunnels in the entire burrow system of each individual Tuco-tuco was measured from the maps and the total above area covered by each individual was also measured from the maps using the minimum convex polygon

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method. The degree of convolution of each burrow system was quantified by dividing the total length of tunnels in the burrow system by its total above-ground area (Cameron et al. 1988).

We arbitrarily designated the longest continuous segment of a burrow as the main tunnel. Any tunnel comming off this segment was considered a branch. Tunnels ending at the surface were named feeding tunnels. Branch angle was measured as the smallest angle between two intersecting segments.

Plant biomass and soil characteristics were measured from samples taken near burrows. Vegetation was collected from a circle around the burrow in five 0.24 m^2 and 30 cm depth samples. Biomass was estimated by separation on aerial and subterranean portions of vegetation that were dried at 80 °C for 24 h. Soil samples were collected at the depth of burrow tunnels. Moisture was determined by differential readings before and after drying soil samples at 80 °C to constant weight. Silt-loam fractions were separated using a sieve set.

Numerical results are given as mean ± S.D. Student's t and χ^2 tests were used to test for significant differences between mean values and proportions, respectively. Discriminant analysis was performed between male and female burrows. Correlations among burrow variables as well as between these variables and soil and vegetation variables were established.

Results

Major features of a male and a female excavated burrow system are shown in Figure 1. Data for 12 female- and 10 male-excavated burrow systems are presented in Table 1.

Table 1. **Body mass and burrow system characteristics of *Ctenomys talarum* from Mar del Cobo, Buenos Aires, Argentina**

Values are given as x ± SD. Numbers in parentheses are sample sizes

Characteristic	Male (n=10)	Female (n=12)	Total (n=22)
Body mass (g)	133 ± 15	104 ± 13	117 ± 20
Burrow length (m)	17 ± 7	11 ± 7	14 ± 8
Burrow area (m^2)	10 ± 8	5 ± 4	8 ± 6
Degree of convolution	2 ± 0.7	2 ± 0.7	2 ± 0.7
Main tunnel length (m)	8 ± 4	5 ± 3	6 ± 4
Branch length (m)	9 ± 4	6 ± 4	7 ± 4
Number of branches	8 ± 6	8 ± 6	8 ± 6
Interfork distance (m)	1 ± 0.4	0.8 ± 0.3	0.9 ± 0.4

Table 2. **Soil humidity and granulometry in mass percent at the excavated burrow location**

Data are given as x ± SD

Soil characteristic	Male (n=10)	Female (n=12)	Total (n=22)
Humidity	5 ± 1	4 ± 2	5 ± 2
Silt (>2 mm)	0.2 ± 0.3	0.7 ± 0.9	0.5 ± 0.8
Very coarse sand (<2 mm >1 mm)	1.3 ± 1.5	2 ± 3	1.6 ± 2
Coarse sand (<1 mm >0.5 mm)	30 ± 6	13 ± 10	21 ± 12
Medium sand (<0.5 mm >0.25 mm)	18 ± 2	39 ± 12	30 ± 14
Fine sand (<0.25 mm >0.125 mm)	44 ± 8	39 ± 9	41 ± 9
Very fine sand (<0.125 mm >0.058 mm)	5 ± 2	5 ± 2	5 ± 2
Loam-clay (<0.058 mm)	1.4 ± 0.7	1 ± 0.5	1.2 ± 0.7

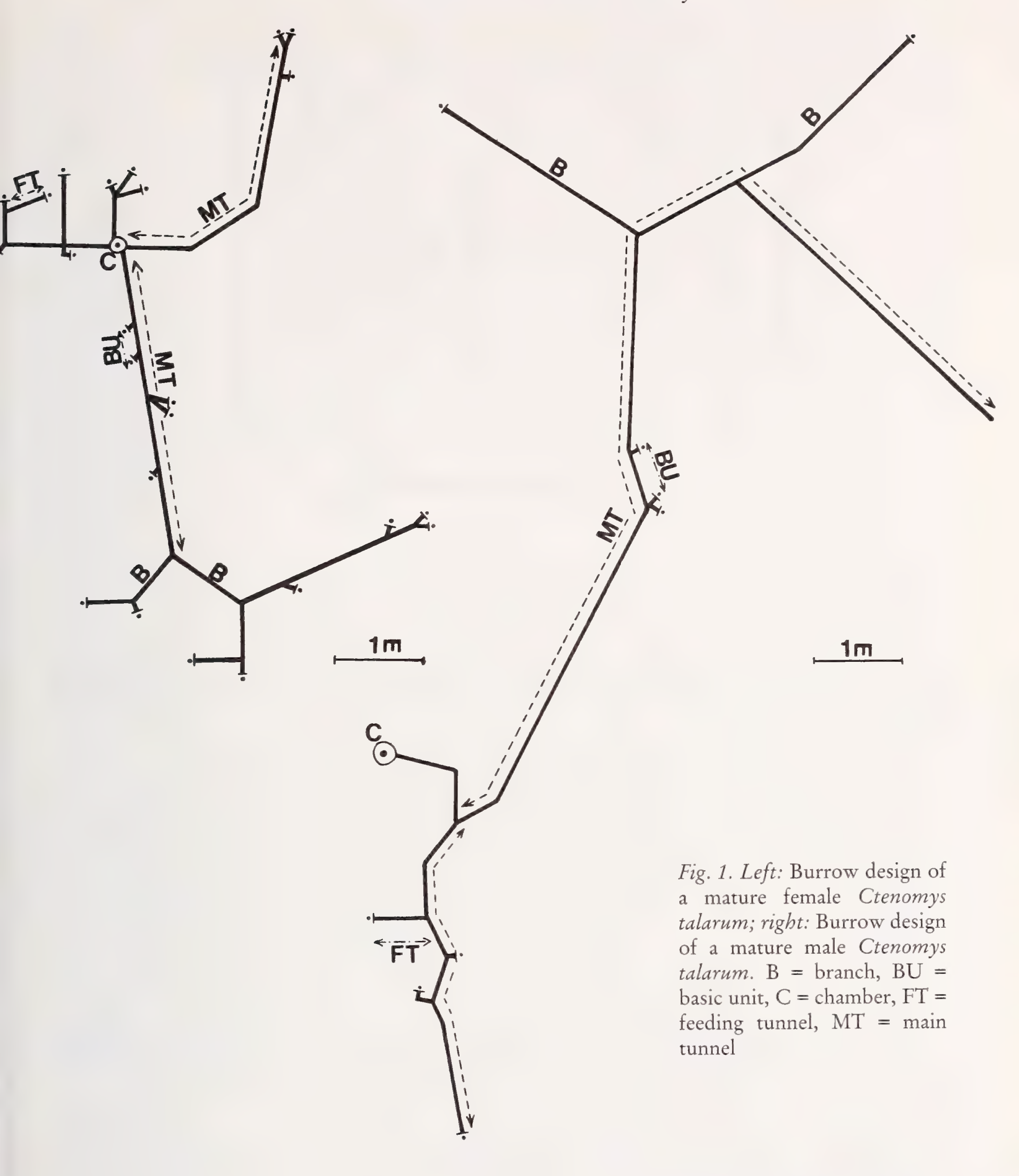


Fig. 1. Left: Burrow design of a mature female *Ctenomys talarum; right:* Burrow design of a mature male *Ctenomys talarum.* B = branch, BU = basic unit, C = chamber, FT = feeding tunnel, MT = main tunnel

The burrow system of *Ctenomys talarum* has a branching structure, consisting primarily of a main axial tunnel that occupies 48 % of the total length and a variable number of lateral branches and feeding tunnels. All tunnels to the surface are plugged and systems never interconnected.

Male and female burrow systems have the same basic design ($0.10 > P > 0.05$). The main tunnel is formed by basic unit buildings (interfork distances) of 0.9 ± 0.4 m. About 48 % of the branching angles were > 40° and clustered around 75° and 90° (Fig. 2). The construction of left- and right-directed segments is statistically different ($P < 0.05$).

Average body weight was significantly different between sexes ($P < 0.001$). Male burrows occupied greater above-ground areas than female burrows ($0.1 < P < 0.05$). We

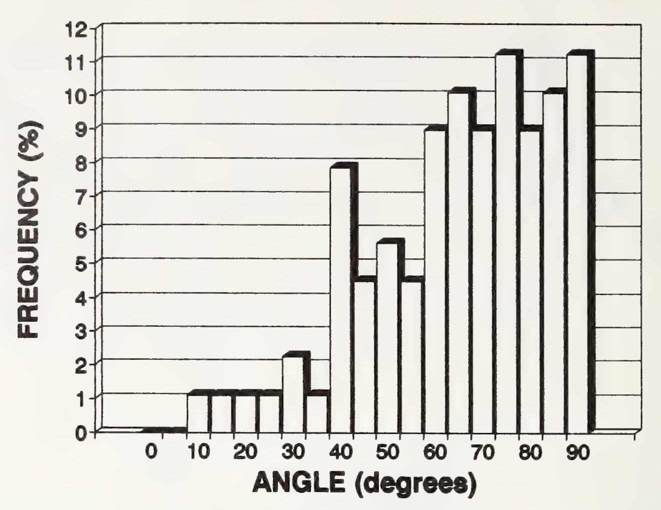


Fig. 2. Frequency distribution of burrow branch angles

did not detect a significant difference in the total length of tunnels, degree of convolution or diameter between burrow systems of male and female Tuco-tuco ($P > 0.1$).

A single nest chamber, packed with dry grasses, was found at the main tunnel in females, and in a blind lateral branch (0.5 ± 0.4 m) in males. Chamber mean diameter was 21 ± 7 cm and was built in deeper tunnels ($P < 0.02$) in males (45.62 ± 6.07 cm) than in females (35.5 ± 8.32 cm).

Table 3. **Plant biomass in g at excavated burrow location**

Data are given as x ± SD

Biomass	Male (n=10)	Female (n=12)	Total (n=22)
Subterranean	313 ± 63	249 ± 148	278 ± 120
Aerial	212 ± 198	350 ± 191	287 ± 202
Total	527 ± 189	647 ± 255	592 ± 231

Soil characteristics and plant biomass at the excavated burrow location are shown in Tables 2 and 3, respectively. Statistically significant correlations exist between a number of burrow parameters and between burrow parameters and habitat characteristics:

Burrow total length is correlated with: number of branches, number of feeding tunnels, animal weight and subterranean plant biomass ($P < 0.05$, $n = 22$).

Main tunnel length is correlated with: number of feeding tunnels, soil humidity and subterranean plant biomass ($P < 0.05$, $n = 22$).

Main tunnel depth is correlated with: number of branches, coarse grain sand, medium grain sand and subterranean plant biomass ($P < 0.05$, $n = 22$).

Tunnel diameter is correlated with: coarse grain sand and medium grain sand ($P < 0.05$, $n = 22$).

The number of branches of the system is correlated with the subterranean plant biomass ($P < 0.05$, $n = 22$).

Features of *Ctenomys talarum* compared to those of other subterranean rodents are reported in Table 4.

Table 4. **Burrow system characteristics of *Ctenomys talarum*, *Cryptomys hottentotus* and *Pappogeomys castanops***

Species Characteristic	*Ctenomys talarum*	*Cryptomys hottentotus*	*Pappogeomys castanops*
Surface (m^2) mounds	14.4 ± 6.7	–	74.0 ± 49.7
Total Length (m)	13.8 ± 7.5	181.0 ± 118.0	75.8 ± 27.0
Tunnel Depth (cm)	13.7 ± 4.1 39.9 ± 9.2	2.2 ± 0.5 49.5 ± 17.1	13.8 ± 4.0 81.8 ± 32.8
Tunnel mean diameter (cm)	8.1 ± 0.9	4.5 ± 0.6	10.2 ± 1.5
Nest chamber deep (cm)	39.9 ± 9.3	18.1 ± 8.9	34.5 ± 7.4
Occupants (n)	1.0 ± 0.0	2.2 ± 0.5	2.0 ± 1.0
Reference	this study	Hickman (1978)	Hickman (1977)

Discussion

As reported for other species of *Ctenomys* (Hickman 1990; Reig et al. 1990) our study shows that burrows of Tuco-tuco are convergent in their main features to those of other unrelated subterranean rodents. Andersen (1988) found that burrow systems of *Geomys* are linked segments of tunnels, and Reichman et al. (1982) suggested that burrow length of *Thomomys* are attained by incorporating burrow segments (one interfork distance and its associated branch). Furthermore, Vleck (1981), examining the energetics of foraging of geomyds, estimated a minimum-cost segment length between 0.6 and 2.4 m. The mean segment length (interfork distance) for Tuco-tuco lies within this interval and was 0.91 ± 0.31 m. Optimal foraging theory predicts the tendency for burrow branches to be orthogonal to the originating tunnel (Andersen 1988). We found that Tuco-tuco branch angles were variable, and greater than 60° (Fig. 2).

Moreover, in concurrence with studies in the family Geomyidae (Hickman 1990), gender did not affect architecture of burrow systems of *Ctenomys.* Although there are only statistically significant differences between male and female burrow areas, there is a tendency for males to occupy more elongated, branched burrow systems.

Position of the nest was reported to be adaptive, multiple entrances increased air circulation and less traffic congestion near the nest when occupied by young, while a central position allows equal foraging and territorial defense (Hickman 1990). Tuco-tuco males placed their nests on a central blind branch, while females have them in the main tunnel. Nest position was more central in heavier females, probably reflecting the burrowing pattern.

Soil type may influence burrow architecture as a mechanism to compensate for differences in the cost of excavating and rate of diffusion of gases. In our study, soil granulometry affected the diameter and depth of the tunnels. Similarly, soil humidity was correlated with main tunnel length of burrow.

Reichman et al. (1982) suggested that elongated, branched burrow systems may be required for resource acquisition in less productive areas. Although we did not find a correlation of burrow parameters to total above-ground biomass, both the length of the burrow and the number of branches were negatively correlated with subterranean biomass.

Field research throughout the year is needed to assess seasonal and reproductive influence on burrow parameters, as well as laboratory studies to estimate the cost of construction.

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Zusammenfassung

Die Struktur der Baue von Ctenomys talarum, einer unterirdisch lebenden Nagerart

Untersucht wurden 22 vollständig ausgegrabene Baue von Tuko Tukos (*Ctenomys talarum*). Die Gangsysteme der Männchen sind im Durchschintt größer und haben die Nestkammer am Ende eines Seitentunnels, wogegen die Weibchen ihr Nest im Hauptgang anlegen. Sonst sind die Baue bei Männchen und Weibchen ähnlich. Sie bestehen aus einem Hauptgang von durchschnittlich 48 % des Gesamtsystems, von dem im Abstand von im Mittel 0,9 ± 0,4 m Seitengänge abzweigen. Die unterirdische Pflanzenmasse pro Volumeneinheit war mit der Baulänge und der Anzahl von Abzweigungen negativ korreliert. Die Korngröße des Bodens beeinflußte den Durchmesser und die Tiefe der Gänge, und die Bodenfeuchtigkeit war mit der mittleren Tunnellänge korreliert.

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Distribution patterns of small mammal fauna along gradients of latitude and altitude in Northern Spain

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Investigated the influence of geographical factors (latitude and altitude) on the distribution of small mammal fauna. We analysed approximately 3000 Barn Owl pellets collected from 20 different localities in Northern Spain. These pellets contained the remains of 9744 small mammals belonging to 17 species. Three groups of species were found: 1. one group associated with latitude (*Sorex coronatus, Neomys fodiens, Clethrionomys glareolus, Microtus pyrenaicus, Apodemus sylvaticus, Mus spretus*), 2. another group related to altitude (*Suncus etruscus, Crocidura russula, Microtus agrestis*), and 3. a third group whose distribution was not affected by latitude or altitude (*Sorex minutus, Eliomys quercinus, Microtus cabrerae, M. nivalis, M. duodecimcostatus, Arvicola sapidus, Rattus rattus, R. norvegicus*).

The distribution of these species is discussed in relation to geographical and climatic factors. Our data demonstrate that latitude is the most important factor in determining the presence of a species at the southern limit of their range.

Introduction

Distribution and diversity of small mammals are affected by geographical factors of which latitude and altitude are the main variables used in zoogeographical studies (Pianka 1966; Bond et al. 1980; Fons et al. 1980; Brunet-Lecomte and Delibes 1984; Delibes 1985; Alcántara 1989; Brünner and Neet 1991).

In Western Europe the number of small mammalian species decreases from north to south (Herrera 1974). It has also been demonstrated that when altitude increases the diversity of small mammals decreases (Abe 1982; Delibes 1985; Alcántara 1989). Variation in altitude may reproduce variation in latitude, so that in this study both gradients are investigated. The aim of the present study was to determine, within a medium altitudinal range, the influence of these two geographical variables on the distribution of small mammals, and at the southern limit the presence of certain species (Corbet 1978).

Material and methods

The study was conducted in the province of Huesca (42°45′–42°05′ N, 00°45′–00°17′ W). Although the latitudinal range is restricted, the orography varies markedly. Altitude ranges from 420 and 987 m above sea level with three distinct geographical regions (see Figure): Ebro Valley (Mediterranean lowlands), pre-Pyrenees (Atlantic lower montane area), and Pyrenees (alpine high mountain area).

The sampling method was the analysis of Barn Owl pellets. In spite of the limitations of this sampling procedure (Saint-Girons and Spitz 1966), it is valid for biogeographical studies of small mammals (Heim de Balsac and Beaufort 1966; Herrera 1974; Brunet-Lecomte and Delibes 1984). We analysed about 3000 Barn Owl pellets collected from 20 different localities (Fig. and Tab. 1) which contained 9744 small mammals. The data gathered are most likely heterogeneous since pellets were collected at different times of the year and pooled together, and although the Barn Owl's diet shows monthly changes (Saint-Girons 1968; Marti 1973; Webster 1973; Herrera 1973), the effect of seasonal changes on the results should be buffered since, of the 20 analyses studied, 12 exceeded 300 prey items (see Herrera 1974 for a similar approach).

Temperature and precipitation data were taken from Elías and Ruíz (1977) for the points nearest to sampling sites.

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Situation of the localities from which Barn Owl pellets were taken. Numbers correspond to the localities as numbered in Table 1

Simple correlation analysis was performed to test for an effect of latitude, altitude, temperature, and precipitation on the geographical distribution of small mammals in the study area. Stepwise multiple regression analyses (Sokal and Rohlf 1981), with the relative abundance of the different taxa as dependent variables, were performed to show which geographical variable (latitude, altitude) primarily affected the distribution of small mammals. Small mammal diversity was calculated using the Shannon-Weaver Index and richness was taken as the number of species in each locality.

Results

In the study area latitude and altitude are highly correlated ($r = 0.767$, $p < 0.001$) however, they do not show the same relation to small mammal distribution, with latitude being more highly correlated for most species.

The raw data are shown in Table 1 where the richness index for each locality is also included. Five insectivorous and 12 rodent species were found. Stepwise multiple regression analyses distinguished three groups of species (Table 2):

1. Species whose distribution is primarily related to latitude (*Sorex coronatus, Neomys fodiens, Clethrionomys glareolus, Microtus (Pitymys) pyrenaicus, Apodemus sylvaticus,* and *Mus spretus*).
2. Species whose distribution is primarily related to altitude (*Suncus etruscus, Crocidura russula,* and *Microtus agrestis*).
3. Species whose distribution is not related to either altitude or latitude (*Sorex minutus, Eliomys quercinus, Microtus cabrerae, M. nivalis, Microtus (Pitymys) duodecimcostatus, Arvicola sapidus, Rattus rattus,* and *R. norvegicus*).

When species were grouped in Orders, latitude was the first variable selected by the stepwise regression analysis (Table 2), being positively correlated with the abundance of Insectivora and inversely correlated with the abundance of Rodentia.

Table 1. **Localities from which pellets were taken and percentages of prey**

LOC	N	ALT	LAT	SM	SC	NF	SE	CR	EQ	CG	MA	MC	MN	MP	MD	AS	APS	MSP	RR	RN	R
1 Hecho	941	843	42° 45′	0.32	7.55	0.11		37.73	0.21	0.43	2.44			2.66	14.13		34.33	0.11			11
2 Navasa	347	987	42° 32′		4.32		0.58	44.96			4.61		0.42		17.29	0.29	17.29	9.80	0.86		9
3 Lavelilla	1196	710	42° 34′		0.67		1.34	23.49	0.08	0.08	0.08				21.82	0.17	47.91	3.68	0.25		12
4 Puente de Fanlo	42	750	42° 30′		2.38		2.38	61.90	2.38			2.38			4.76		16.67	7.14			8
5 Arto	396	800	42° 27′		4.29		0.76	37.12	0.25		2.53	0.25			12.63		28.03	14.14			9
6 Orna de Gállego	52	769	42° 27′		1.92			30.77			3.85	1.92			32.69		23.08	5.77			7
7 Javierrelatre	326	709	42° 24′		13.80		2.15	46.93			3.99	2.15			2.15		18.10	10.74			8
8 Aquilué	171	689	42° 22′	0.58	11.11			21.64	2.34		0.58				17.54		38.60	7.60			8
9 San Vicente	272	802	42° 21′		7.72		0.74	40.81			1.84				12.50		30.15	6.25			7
10 Arascues	442	673	42° 14′				0.45	21.72			0.23				8.37		10.41	58.82			6
11 Igriés	719	601	42° 12′				1.53	14.46	0.14		0.14				27.96		10.99	44.37	0.42		8
12 Sta. Eulalia la Mayor	465	867	42° 12′		0.22		0.43	27.96	0.22						16.34		23.87	30.97			7
13 Castilsabás	964	722	42° 11′	0.10			1.68	20.44	0.10						19.18	0.52	16.88	40.88	0.21		9
14 Otura	242	462	42° 09′				0.41	4.13							23.97		5.37	66.12			5
15 Alerre	1723	500	42° 09′				4.99	14.74							19.04	0.23	9.81	51.19			6
16 Huerrios	377	487	42° 08′				4.51	28.65							11.67	0.27	13.53	41.11		0.7	7
17 Banaries	198	472	42° 08′				15.15	17.68							9.60		4.55	53.03			5
18 Torres Secas	217	490	42° 08′				0.92	20.28	0.46						23.50	2.30	19.35	33.18			7
19 Pompenillo	128	420	42° 05′				4.69	10.94							1.56		9.38	72.66	0.78		6
20 Monflorite	515	436	42° 05′				1.17	13.98	0.19						43.69	0.19	10.10	30.49	0.19		8

Abbreviations: N = number of prey, ALT = altitude (m a.s.l), LAT = latitude, SM = *S. minutus*, SC = *S. coronatus*, NF = *N. fodiens*, SE = *S. etruscus*, CR = *C. russula*, EQ = *E. quercinus*, CG = *C. glareolus*, MA = *M. agrestis*, MC = *M. cabrerae*, MN = *M. nivalis*, MP = *M. pyrenaicus*, MD = *M. duodecimcostatus*, AS = *A. sapidus*, APS = *A. sylvaticus*, MSP = *Mus spretus*, RR = *R. rattus*, RN = *R. norvegicus*, R = Richness.

Table 2. **Stepwise multiple regression analyses of species distribution showing the first selected variable, the partial correlation coefficient (r) and the significance level (p)**

Species	Variable	r	p
S. minutus	–	–	–
S. coronatus	latitude	0.55	0.05
N. fodiens	latitude	0.55	0.05
S. etruscus	altitude	−0.47	0.05
C. russula	altitude	0.70	0.01
E. quercinus	–	–	–
C. glareolus	latitude	0.61	0.01
M. agrestis	altitude	0.64	0.01
M. cabrerae	–	–	–
M. nivalis	–	–	–
M. pyrenaicus	latitude	0.55	0.05
M. duodecimcostatus	–	–	–
A. sapidus	–	–	–
A. sylvaticus	latitude	0.70	0.01
R. rattus	–	–	–
R. norvegicus	–	–	–
Mus spretus	latitude	−0.82	0.01
Insectivora	latitude	0.66	0.01
Rodentia	latitude	−0.64	0.01
Richness	latitude	0.73	0.01
H′	altitude	0.57	0.01

Richness and diversity (H') were positively correlated with both geographical variables, but the former was primarily related to latitude and the latter to altitude.

Discussion

In the present study three geographical zones could be differentiated: Pyrenees, pre-Pyrenees, and Ebro Valley. These important physiographic variations are accompanied by parallel variation in temperature, precipitation (Elías and Ruíz 1977), and vegetation (Peinado and Rivas-Martínez 1987). All of these factors highly affected the distribution of small mammals in this area.

The distributions of *S. coronatus, N. fodiens, C. glareolus, M. pyrenaicus, A. sylvaticus* and *Mus spretus* are primarily related to latitude. All these species, except *A. sylvaticus* and *Mus spretus*, have Eurosiberian distributions (Saint-Girons 1973; Amori et al. 1984; Hausser et al. 1985) and the south slope of the Pyrenees constitutes the southern limit of their distribution. As expected, they show a positive correlation with latitude, increasing in abundance from the Mediterranean to the Eurosiberian region. In spite of the few individuals found for some species (i. e., *N. fodiens* and *C. glareolus*), the positive correlation with precipitation ($p < 0.01$ in all cases) and negative with temperature ($p < 0.01$ in *N. fodiens* and *C. glareolus*; $p = 0.06$ in *S. coronatus*) seems to indicate that a general trend exists in these species for inhabiting areas with a balanced Atlantic climate.

The distributions of *A. sylvaticus* and *Mus spretus* are also primarily related to latitude, the former being directly correlated and the latter inversely. In France and Spain *Mus spretus* shows an increase in abundance to the south (Saint-Girons and Vesco 1974; Brunet-Lecomte and Delibes 1984). It appears from this study that *Mus spretus* requires Mediterranean conditions, as its distribution is positively correlated with temperature and negatively correlated with precipitation ($p < 0.01$ in both cases; see also Thaler et al. 1981). *A. sylvaticus*, however, shows a clear positive gradient northwards, with its

distribution directly correlated with precipitation ($p < 0.01$) but unrelated to temperature ($p = 0.2$). ALCÁNTARA (1989) pointed out that the distribution of this species is related to habitat structural features. Given the latitudinal variation of vegetation in the study area (PEINADO and RIVAS-MARTÍNEZ 1987), our results may reflect such variation in habitats.

The distribution of *C. russula, S. etruscus,* and *M. agrestis* is related to altitude. *Crocidura russula* increases with altitude. The general trend for Crocidurinae is, on the contrary, to inhabit temperate lowland areas (ABE 1982; ALCÁNTARA 1989; BRÜNNER and NEET 1991). This apparent contradiction to general findings might be explained by considering the unusual kind of habitat preference exhibited by *C. russula* in the mountain areas of western Europe, where its presence is restricted to the vicinity of human dwellings (CHURCHFIELD 1990) rather than being influenced by any geographical factors. *S. etruscus* decreases with altitude, in accordance with the general distribution of European Crocidurinae (CHURCHFIELD 1990). *M. agrestis* increases at higher altitudes, following the general trend shown for this species in Spain (DUEÑAS and PERIS 1985; DELIBES 1985).

The distributions of *S. minutus, E. quercinus, M. cabrerae, M. nivalis, A. sapidus, M. duodecimcostatus, R. rattus*, and *R. norvegicus* are not affected by either altitude or latitude. *S. minutus* has been shown as a species inhabiting altitudes above 1000 m a.s.l. in the Pyrenees (VERICAD 1970; GOSÁLBEZ and LÓPEZ-FUSTER 1985); however, in our study area, where all sites are lower, its distribution is not affected by altitude. DELIBES (1981) did not find any correlation between altitude and the distribution of this species in the eastern Cantabric Mountains (North of Spain). In spite of the small number of individuals found in our study, the results seem to suggest that the main factor affecting the distribution of this species is humidity, rather than altitude, since its distribution is positively correlated with precipitation ($p = 0.02$; see GOSÁLBEZ 1976 for a similar result).

Arvicola sapidus, E. quercinus, R. rattus, and *R. norvegicus* are widely distributed in Spain. Their distribution does not seem to be related to geographical factors, but (with the exception of *E. quercinus*) to the presence of water-bodies or human habitation (GOSÁLBEZ and LÓPEZ-FUSTER 1985).

In Spain, *M. duodecimcostatus* has a typical Mediterranean distribution (SANS-COMA et al. 1973). Absence of relatedness with all variables considered in this study supports the suggestion of GOSÁLBEZ et al. (1985) that *M. duodecimcostatus* is distributed according to the nature of the ground rather than on any geographical factor.

The distribution of *M. cabrerae* and *M. nivalis* is not related to latitude or altitude, but is likely to be restricted to localised habitats in Spain (GOSÁLBEZ and LÓPEZ-FUSTER 1985), e. g. rockslides for *M. nivalis* and rush for *M. cabrerae*.

Insectivora increase with latitude while Rodentia decrease. These results agree with those by HERRERA (1973), CHEYLAN (1976), and BRUNET-LECOMTE and DELIBES (1984), who found a decline in the proportion of Insectivora southwards in Europe. This trend may be explained by the boreal origin of most of these species (HAUSSER et al. 1985).

Generally, diversity decreases with altitude (e. g. MARTÍN and VERICAD 1977; BLONDEL et al. 1978; ABE 1982; ALCÁNTARA 1989) since high mountains have an island effect (MCARTHUR 1972). Our results, however, are in contradiction to this general trend in that diversity increases with altitude. Such disagreement may be explained by the altitudinal range of the study area, which probably represents an ecotone (HOFFMANN 1984); i. e., the lowest limit for high altitude species and the highest limit for low altitude species (see DUEÑAS and PERIS 1985 for a similar result).

Latitudinal gradients in richness are well known, with species numbers decreasing as latitude increases (HERRERA 1974; MCCOY and CONNOR 1980). Our results, however, show an increase in richness as latitude increases. Similar to the trend in diversity, it could be argued that such an increase is the consequence of the border effect (MCARTHUR 1972), due to the Eurosiberian distribution of the species.

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Zusammenfassung

Verteilung der Kleinsäugerfauna entlang von Breiten- und Höhen-Gradienten in Nordspanien

Es wurde der Einfluß der geographischen Breite und der Höhe über NN auf die Verbreitung von Kleinsäugern untersucht. Annähernd 3000 Schleiereulengewölle von 20 verschiedenen Orten Nordspaniens wurden untersucht. Diese Gewölle enthielten Überreste von 9744 Kleinsäugern aus 17 Arten. Diese Arten konnten drei Gruppen zugeordnet werden: 1. Beziehung zur geographischen Breite (*Sorex coronatus, Neomys fodiens, Clethrionomys glareolus, Microtus pyrenaicus, Apodemus sylvaticus, Mus spretus*), 2. Beziehung zur Höhe über NN (*Suncus etruscus, Crocidura russula, Microtus agrestis*), 3. Keine Beziehungen zu geographischer Breite und Höhe über NN (*Sorex minutus, Eliomys quercinus, Microtus cabrerae, M. nivalis, M. doudecimcostatus, Arvicola sapidus, Rattus rattus, R. norvegicus*).

Die Verteilung der Arten wird in Beziehung zu geographischen und klimatischen Faktoren gesetzt. Unsere Daten zeigen, daß die geographische Breite der für das Auftreten von Arten nahe ihrer südlichen Verbreitungsgrenze bedeutendste Faktor ist.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

The use of fur colour characters to distinguish the sibling species *Sorex araneus* and *Sorex coronatus* (Insectivora, Soricidae): a field test in a zone of parapatric contact

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In their description of *Sorex coronatus* Millet, 1828, Meylan and Hausser (1978) showed that this species, previously named *S. gemellus* by Ott (1968), is distinguished from the closely related sibling species *Sorex araneus* on the basis of its karyotype (see Hausser 1990; Hausser et al. 1990, for a detailed review of the literature on these two species). Although very clear differences in mandible morphology have been found between *S. araneus* and *S. coronatus* (e.g. Hausser and Jammot 1974; Handwerk 1987) and although several biochemical characters may be used to separate many of the chromosomal races of *S. araneus* from the unique chromosomal race of *S. coronatus* (Catzeflis et al. 1982; Catzeflis 1984; Hausser and Zuber 1983; Neet and Hausser 1989, 1991), the only absolute difference between these sibling species that permits to distinguish them throughout their whole biogeographical range remains the karyotype.

However, for field identifications, morphological characters are necessary. Some possible characters such as tail and hindfoot lengths have been discussed by Ott (1968), Ott and Olert (1970) and Handwerk (1987), but these characters are not clearcut enough to provide a useful field identification criterion.

Differences in fur colour patterns of *S. araneus* and *S. coronatus* were first noticed by von Lehmann (1955) and Olert (1969). A consistent description of these patterns was given by Ott and Olert (1970) and Olert (1973a, b), who defined *S. araneus* as a darker species with a broad dark back band, while *S. coronatus* has a narrow dark back band, with lighter flanks and a tricolorous aspect. Olert used techniques such as optic densitometry to demonstrate that these fur colour differences can be quantified (Olert 1973a). Differences were actually quite obvious in some localities, enabling Ott and Olert (1970) to obtain 100 % correct identifications with n = 8 individuals sampled from the Swiss Alps. Nevertheless, Meylan and Hausser (1978) have considered that fur colour characters are probably too variable to be of any general value to discriminate *S. araneus* from *S. coronatus*. Our own observations have shown that when one gains some experience and practice in identifying these two species frequently by use of karyological or biochemical techniques, fur differences can be observed and some individuals appear to be clearly identifiable, especially when dealing with typically tricolorous *S. coronatus* specimens.

In order to assess to what extent fur colour characters can be considered to be reliable for field identifications, we undertook a test in a zone of parapatric contact between the two species during the summer 1987. The contact zone is situated on the border of the lake of Neuchâtel (Switzerland) and has been described by Neet and Hausser (1990). The test

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Percentages of individuals of *Sorex araneus* and *S. coronatus* correctly identified during field tests using fur colour characters, and tests of the deviation of the numbers of correctly (I_c) and erroneously (I_w) identified individuals from a null hypothesis of randomness

Field test period	% of correct identifications	n_a	n_c	I_c	I_w	χ^2	p
15.–16. 9. 1987	84.6	36	16	44	8	14.16	0.0002 ***
22.–23. 9. 1987	66.7	8	10	12	6	1.03	0.31 N.S.
28.–29. 9. 1987	73.2	27	14	30	11	4.65	0.03 *
Mean	74.8						

n_a = number of *S. araneus* in the test, n_c = number of *S. coronatus* in the test, N.S. = nonsignificant, * = $p < 0.05$, *** = $p < 0.001$.

simply consisted of identifying individuals at night, during trap controls, with a torch lamp. The tests were carried out in trapping areas that had not been visited more than once before the onset of testing and thus, there was no particular knowledge of the individuals encoutered. The fur colour characters mentioned above were used for these identifications. As individuals were systematically marked and identified by serum albumin electrophoresis (Neet and Hausser 1989), the field identifications could be controlled *a posteriori*. As shown in the Table, a mean correct identification rate of about 75 % was obtained over three independent tests. This rate indicates that differences are detected in field conditions since the mean correct identification rate clearly exceeds the 50 % level that would be expected under a random rate of species attribution. However, results in the Table also show that only two out of three tests gave significant deviations from a null hypothesis of random species attribution, and the maximal proportion of correct identifications obtained still left 15 % erroneously identified specimens.

Thus, we conclude that fur colour characters are not very efficient and are only of limited value to distinguish *S. araneus* and *S. coronatus* under usual field conditions.

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On a Fishing cat, *Felis (Prionailurus) viverrina* Bennett, 1833, from continental Malaysia

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In 1967 the aborigines in Bahau Negeri Sembilan (about 2° 40′ N, 102° 36′ E) captured a spotted cat about the size of a large domestic cat. The animal was given to the Melaca Zoo where it arrived on 9 June 1967 and where it died on 25 April 1977. Then the cat was mounted and sent to the Wildlife Training Centre at Bukit Rengit, Lancang, Pahang, where it still can be found (see figure).

The specimen had a rather course earthy-grey fur with body markings consisting of a series of elongate spots arranged in more or less longitudinal rows. The tail was less than 50 % of the head and body length. The total length of the mounted animal was about 770 mm, the tail length about 280 mm. The general build was rather stocky with comparatively short legs and a rather elongated head.

From the description and the photograph it is evident that the animal is a fishing cat, *Felis (Prionailurus) viverrina* Bennett, 1833. So far, the species has not been mentioned for the fauna of continental Malaysia (see e.g. Medway 1969, 1978; Harrison 1966) and thus the Bahau Negeri Sembilan specimen is the first one known from the Malay Peninsula.

Is the fishing cat a new faunal element for the Malay Peninsula or has the species always been present in small numbers but has gone unnoticed or are we dealing with escaped specimens kept as pets or in Zoos? These are questions which cannot be answered with certainty.

It is, however, clear that the species has a rather unusual distribution. It occurs with isolated populations in southern India and Sri Lanka. The major distribution is from Nepal through western India and Burma to the northern half of Thailand and Indo-China



Mounted fishing cat, *Felis viverrina* Bennett, 1833, caught in Bahau Negeri Sembilan in 1967

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(Pocock 1939; U Tun Yin 1967; Lekagul and McNeely 1977; Van Peenen 1969). Furthermore, it is found in northern and western Java, Indonesia. It is said to occur also on Sumatra but no museum specimens are known from that island.

The isolated occurrence on Java has been explained as an introduction during the Middle Ages, when there was an important cultural and religious invasion to the islands of Sumatra, Java and Bali from India. A large number of buildings (mostly temples) on the islands are still proof of that invasion. It has been argued that the leopard, *Panthera pardus*, the fishing cat, the black-naped rabbit, *Lepus nigricollis*, and the green peafowl, *Pavo muticus*, were then brought to Java for religious and/or cultural reasons.

Another explanation might be that the species originally had a much larger distribution and that we at present only observe relict populations. In the National Natural History Museum at Leiden, the Netherlands, there is a fishing cat collected by P. Diard in Singapore in 1819 (Brongersma 1935), and in the Zoological Reference Collection in Singapore there is a mounted fishing cat, said to be collected at Pontianak, Kalimantan (Borneo), Indonesia in 1880. Till now the Leiden and Singapore specimens were thought to be wrongly labeled but it cannot be excluded that they came from (small) populations that exist no longer. Also must be mentioned a fishing cat said to be shot at Megaran, Bali, Indonesia, some time before 1957 (Meissner 1958). The remains of the specimen, however, have not been studied by a zoologist, so this remains a doubtful record.

Whatever the correct explanation might be, it is worthwhile to pay attention to the occurrence of fishing cats in the Malay Peninsula and in Indonesia (Borneo and Sumatra).

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Occurrence of a melanistic Common vole, *Microtus arvalis* (Pallas, 1779) in Slovakia

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On September 23, 1989 we succeeded in capturing a melanistic specimen of the common vole *(Microtus arvalis)* in a potato field near the village Matejovce (near Poprad, in northern Slovakia) at an elevation of 700 m a. s. l. The specimen was caught accidentally during voluntary works of students on potato fields. It is stored in deposit of the Department of Zoology, Faculty of Sciences, Comenius University, Bratislava as a skin preparation and the skull (damaged). On the basis of the body length (Šebek 1959) its age is estimated at about 3 months.

Description of colouring: dorsal hair – upper part dark, lower part grey-black; ventral hair – grey. Colouring on the head partially changes from dark to dark-grey-brownish.

Niethammer and Krapp (1982) describe 10 colour mutations of *Microtus arvalis* including a melanistic one. Its description was originally given by Reichstein (1957) and Frank and Zimmermann (1957) who also made a follow-up study of the progeny of melanistic voles under laboratory conditions. The latter manifested decreased reactivity, biting, vitality and growth rate and increased mortality rate in the young. A similarly coloured melanistic specimen of *Microtus arvalis* has been described lately by Dolch and Jaschke (1991) from Germany.

The present specimen is to our knowledge the fourth melanistic *Microtus arvalis* mentioned from Central European areas. From Czecho-Slovakia, only its albinotic anomalies have been described so far (Heráň and Mazák 1976; Štusák 1987) and no melanistic *Microtus arvalis* has been reported. The same is true for Poland (Pucek pers. comm.), Hungary (Csorba, pers. comm.), and Austria (Spitzenberger, pers. comm.).

Colour anomalies in small mammals are explained in connection with effects of ecological factors (particularly humidity) (e. g. Simroth 1905; Hanák 1957; Blossom 1942), but also as being genetically determined (e. g. Reichstein 1957; Frank and Zimmermann 1957; Searle 1968). Here, the symbol "a" (recessive) accounts for the melanistic colouring.

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Faecal pellet size differences as a field criterion to distinguish between the two *Ctenodactylus* species (Mammalia, Rodentia)

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The Ctenodactylidae are among the oldest rodent families (Beintema et al. 1991). They are an ecological enigma as well as being a phylogenetic curiosity. The five living species are diurnal although they are to be found in desert or semi-desert conditions in Africa (George 1974). *Ctenodactylus gundi* and *C. vali* inhabit the rocky districts of the northern part of the Sahara. A preliminary study of their range in Algeria has shown that they occupy the Saharan Atlas from Tunisia to Morocco and the wadi Saoura basin to Kerzaz in the south. This range shows no discontinuity and, at first, we were unable to distinguish boundaries between the two species (Gouat and Gouat 1984). More recently, using the method described below, the two species were shown to be parapatric in Algeria (Gouat 1988).

Several criteria for species identification have been proposed in the literature (see George 1982, for review) but none of them is easy to use in the field. One of these criteria is based on the difference in size between the two species, *C. gundi* being slightly larger than *C. vali*. Though these species are diurnal, the difference in size is too small to be clearly identified by direct observation. In addition, gundis are very difficult to trap and body measurements are difficult to obtain.

A gundi site is often identified by numerous piles of droppings left by the annimals at the entrance of their rocky shelters. Fresh droppings are black cylinders 3.5 to 4.2 mm in diameter. They become white with age. In captivity a *C. vali* fed ad libitum on fresh vegetables produces 100 to 250 droppings per day in groups of 10 to 30. According to the difference in body size between the two species, a difference in the size of the droppings was to be expected.

To test this hypothesis, samples of fresh droppings were collected in different sites distributed throughout the range in Algeria (see Table). The species occupying each site was identified according to one or several of the criteria as described by George (1982).

In order to study the influence of the water content of vegetation which decreases from north to south, three *C. gundi* sites (Ferkous, Djemina and Aures 3) were located in the Aures mountains at different latitudes. For similar reasons, samples were collected at different periods of the year on a specific site for each species (Djemina for *C. gundi* and Djeniene Bou Rezg for *C. vali*).

The results are summarized in the Figure. *C. gundi* droppings are longer than the *C. vali* ones. In all the cases but one, the standard error intervals of samples of each species, do not overlap. The only exception is between the *C. gundi* Aurès 3 sample (mean length: 9.62 mm ± 0.50) and the *C. vali* Djeniene Bou Rezg 1 (B1) sample (mean length: 8.90 mm ± 0.27). The difference between these two samples is, nevertheless, significant ($t = 2.30$, $df = 88$, $p < 0.05$).

This study demonstrates that even if there are intra-specific variations in the length of droppings, according to the season or to the site, coprometry is a good criterion for field

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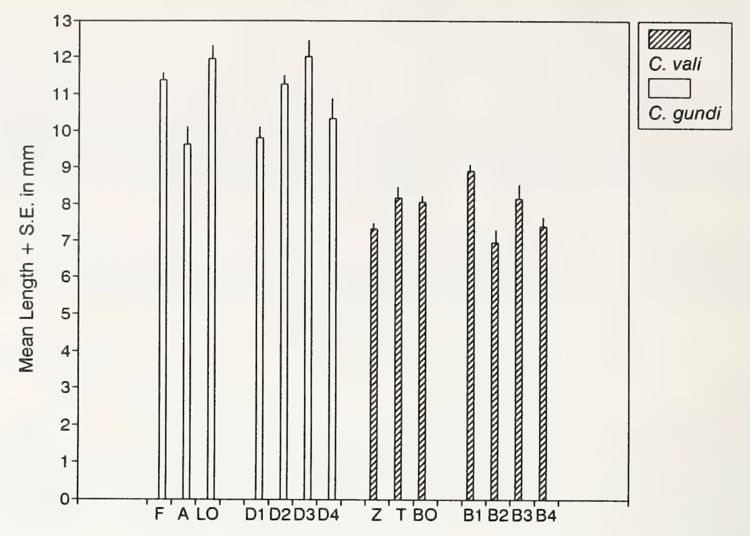


Fig. 1. Mean length (+ S. E.) of different samples of droppings of *C. gundi* and *C. vali.* Each sample is identified by a code name (see Tab. 1 for legend)

diagnosis between the two *Ctenodactylus* species. The samples must be large enough (at least 30 droppings) to be representative but they may be comprised of old white droppings. Droppings are very dry when emitted and their length does not seem to be significantly affected by age. This quality allows us to identify the species which has occupied an abandoned site, and is of great interest when the fluctuations of geographic distribution are studied. The above method might be very efficient in assessing the exact boundaries between these two species in Morocco and in Libya.

Table 1. **Geographic distribution of the collecting sites**

For each sample are given the name of the site, the date of collecting of the sample, the sample size, the geographic coordinates of the site, its altitude and an identification code

	Date of sampling	Sample size	Long. North	Lat.	Alt. in m	Code
C. gundi						
Les Oglats	12. 01. 84	100	32° 23′	0° 37′ W	950	LO
Ferkous	04. 04. 84	100	30° 10′	6° 22′ E	1700	F
Aures 3	03. 05. 85	50	34° 50′	6° 23′ E	450	A
Djemina	25. 12. 83	100	34° 54′	6° 23′ E	550	D1
	05. 05. 84	80				D2
	10. 11. 84	55				D3
	03. 05. 85	50				D4
C. vali						
Zeghamra	10. 01. 84	100	30° 10′	2° 33′ W	740	Z
Taghit 3	11. 01. 84	100	31° 05′	2° 10′ W	600	T
Beni Ounif	12. 01. 84	100	32° 01′	1° 14′ W	800	BO
Djeniene	11. 05. 84	40	32° 18′	0° 53′ W	1100	B1
Bou Rezg	23. 11. 84	40				B2
	05. 01. 85	40				B3
	10. 05. 84	40				B4

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One-year tracking data and behaviour of a released hand-reared Moose *(Alces alces)* in Forest Lapland

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It is evident that moose *(Alces alces)* perform seasonal return migrations between winter and summer habitats which can be 15 km or more apart (Zhirnov 1969; Pulliainen 1974). At the same time, the moose provides evidence for the basic concepts of the familiar area hypothesis (see Pulliainen 1974; Baker 1978). In this context the natural behaviour of moose which have not learned the traditional migration patterns from their mothers are of special interest.

An opportunity arose in the spring of 1989 to carry out an experiment of this kind by releasing into the wild conditions of Finnish Forest Lapland a moose which had lost its mother as a newly born calf in a traffic accident and had been raised in captivity at the zoo attached to the Department of Zoology at the University of Oulu. The animal had been hand-reared to the extent that it had totally lost its shyness towards human beings.

The moose, a female called Suvi, was taken to the northernmost part of the district of Salla in southeastern Finnish Forest Lapland adjacent to the Soviet frontier on October 4, 1990 and released, furnished with a radio transmitter on a collar. This area is characterized by coniferous, mixed and birch forests of the taiga type and isolated fells and marshes of varying size. The release site is one of the overwintering centers for moose in this region (Pulliainen 1974). Suvi was followed as closely as possible after her release. She occasionally disappeared, but always reappeared. The one-year tracking data are shown in the figure. The most interesting observations were as follows:

5-7. 10. 1990: Moved in a very restricted area, was lame in her right fore-leg, was probably feeding on willows; 18. 10.–1. 12.: Was seen with a herd of semi-domestic reindeer on 22. 10. and with a herd of three male moose six days later. Suvi allowed the observer to touch her, but the others escaped to a distance of about 30 m. These moose soon left Suvi, and she then moved about alone, although she was seen with an adult female moose on 1. 12. She had been feeding on juniper. Suvi came to greet both our technicians and a group of hunters (who did not kill her), and eventually all of them ran away; 10. 12. 1990–15. 3. 1991: At the beginning of this period Suvi was together with the female mentioned above, but after the turn of the year she was seen together with three and then four other moose. They had been feeding on juniper and birch. All the moose escaped to a distance of some tens of metres (the technicians were travelling by snow scooter). In late January–early March Suvi was alone, feeding on pine, birch and juniper. For some time she had difficulties with snow which had frozen on her head and kept at a distance of 9–10 m; 22.–26. 3.: Suvi was alone and had been feeding mainly on pine (also some birch); 4.–18. 4.: Suvi was seen three times together with an adult female and her calf. All of them ran away from the snow scooter. They had been feeding on pine and birch; 30. 4.–28. 5.: Suvi was still with the adult female and her calf. They had been feeding on pine and juniper; 5.–25. 6. Suvi was found alone (the adult female had probably given birth to a new calf). Suvi now followed our technicians in the forest and was seen feeding on willows,

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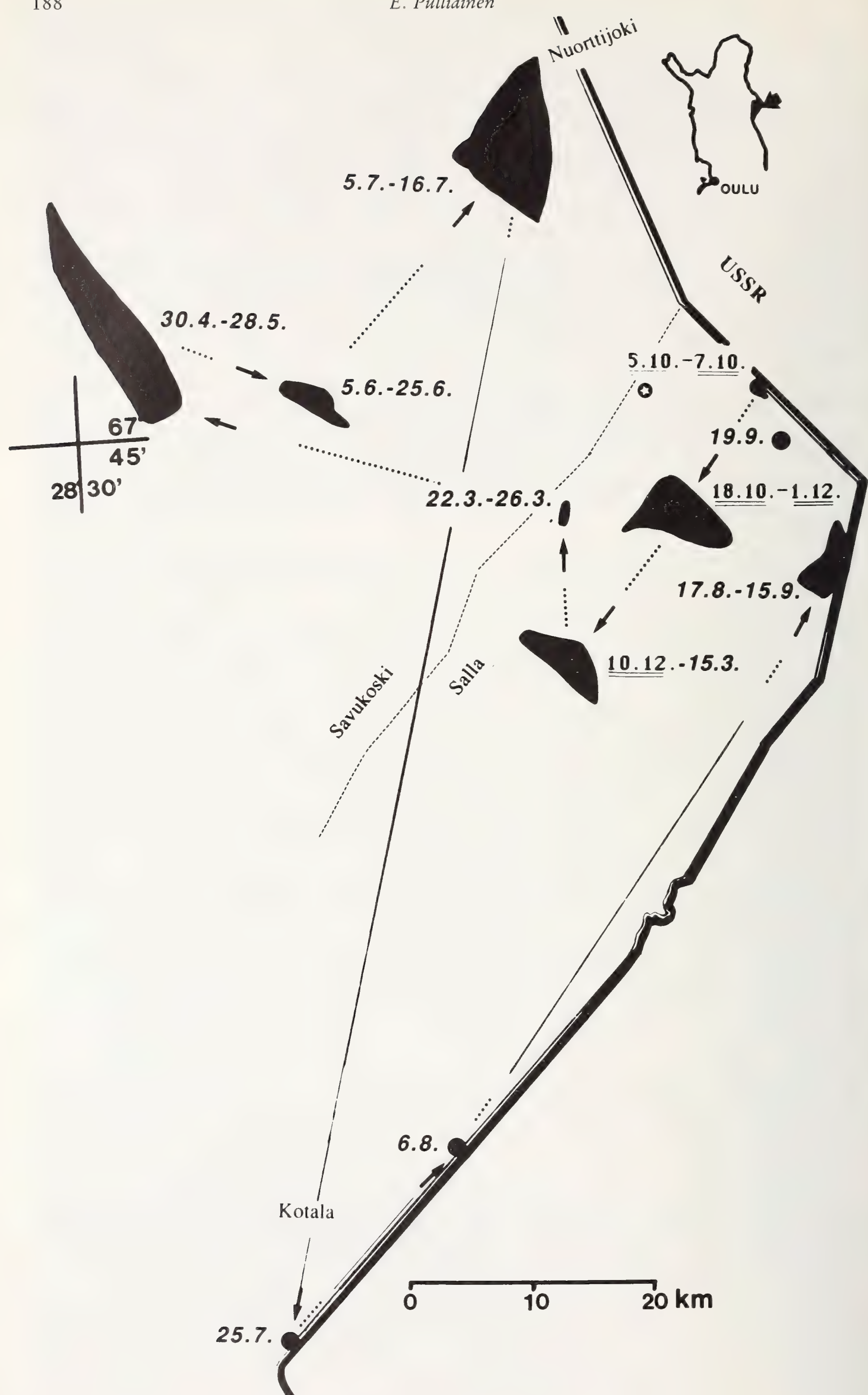
birch leaves and cowberries. She was in a rather poor condition; 5.–16. 7.: Suvi was still alone and was seen feeding on birch leaves. She did not come near the technicians; 25. 7.: A frontier guard saw Suvi alone at a point about 100 km away from the previous observation site. Suvi had covered this distance in 9 days at the most; 6. 8.: Again a frontier guard sited Suvi alone; 17. 8.–15. 9.: On the 17th of August Suvi was together with six male and one female moose, but she was alone again on the 20th of August and came to greet the technician and followed him for 300 m. She was feeding on willows and fireweed, *Epilobium angustifolium.* On 23rd of August she was together with an adult male, and now ran away to a distance of 150 m. Three days later the number of her companions had increased to three, the flight distance remained the same. One of them was a male. On the 31st of August she was again seen with three other moose (two adult males and a yearling), and three days later with four adult male moose, all of which ran away. On the 19th of September Suvi was alone and came to look at the technician, allowing him to touch her.

Suvi's life in the wild began in an interesting way, since she first joined a herd of semi-domestic reindeer, having seen reindeer previously in the nearby enclosures in the zoo but no other moose. She soon discovered her real conspecifics, however, and later on sought only the companionship of other moose, although large numbers of reindeer were grazing in the same area. She tended to join all kinds of groups of moose and then leave them again (or be rejected for some reason). This also means that wild moose accepted Suvi into their group, at least for a time.

Suvi was faced with a difficult decision when accompanying other moose, as a human being approached. Usually an animal such as a moose will either flee or attack when approached by a wolf, for instance, but here the choice was between escape and approaching the human being, to which she had been conditioned in her early life. Usually Suvi ran away with the wild moose, but soon afterwards, when alone, she would come to greet the technician. It is significant that one year of life in the wild did not change her attitude towards human beings to any extent. She remembered their habits, and all her associations acted in favour of continuous companionship with human beings. It is also noteworthy that the other moose associated with Suvi also showed a surprising short flight distance, even as short as 30 m. CEDERLUND et al. (1981), among others, recorded flight distances varying between 200 and 300 m depending on the approach pattern of human beings. Perhaps in the case of Suvi her presence and behaviour towards human beings shortened the flight distance of the other moose.

Our earlier research has shown that the local moose can be classified into two ecological groups, residents and migrants (PULLIAINEN and LOISA 1967; LOISA and PULLIAINEN 1968; PULLIAINEN 1974). The releasing site, at Tuntsa, has long been a typical overwintering area for moose (VESTERINEN 1940; PULLIAINEN 1974), and moose were overwintering there on this occasion as well. The majority of the local moose migrate to the south or southwest in the spring, however (VESTERINEN 1940; PULLIAINEN 1974), and Suvi spent the summer alone in the area to the west, which also is a typical overwintering area. In late July she suddenly moved a hundred kilometres further south to an area where many moose spend their summers, to return to Tuntsa in August, meeting a group of moose which had either spent their summer there or migrated to the overwintering area. We had found earlier that the autumn migration can commence before there is any snow on the ground (PULLIAINEN 1974).

We have carried out many investigations into the food biology of the moose in this area (PULLIAINEN and LOISA 1967; LOISA and PULLIAINEN 1968; PULLIAINEN et al. 1968; TANHUANPÄÄ and PULLIAINEN 1975), and the present observations support our previous findings on the diet of the moose during different seasons.


Nuorttijoki
OULU
USSR
5.7.-16.7.
30.4.-28.5.
5.6.-25.6.
67
45'
28 30'
5.10.-7.10.
19.9.
18.10.-1.12.
22.3.-26.3.
17.8.-15.9.
10.12.-15.3.
Savukoski
Salla
6.8.
Kotala
25.7.
0
10
20 km

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Fig. Movements of the moose Suvi between the 5th of October 1990 and the 19th of September 1991. Movements are indicated with arrows and dotted lines. Black areas with dates are the minimum areas in which Suvi lived during the period in question (dates in 1990 underlined). For further details, see text

BUCHBESPRECHUNGEN

HERHOLDT, ELIZABETH M. (ed.): **Natural History Collections: Their Management and Value.** Transvaal Museum Special Publication No. 1. Pretoria: Transvaal Museum Bookshop 1990. 172 pp., US$ 40,–. ISBN 0-907-99011-8

This book, which was edited by the manageress of th mammal collection of Transvaal Museum in Pretoria, South Africa, contains 15 contributions of South African museologists and two of US American authors. At least seven of the papers pubished in this book are of relevance to mammalogists.

In her article on vertebrate collections E. M. HERHOLDT gives a personal account of specimen preservation, storage, fumigation, general security, documentation and policies and procedures that have to be applied to make the collection available to research.

Very practical aspects are dealt with by F. C. DE MOOR, who discusses different types of containers for wet collection and E. DE WET et al., who address the problem of cleaning and degreasing bone material. It is an important aspect of the latter paper that long-term effects of these techniques are evaluated. The authors also recommend different types of data sheets that help to document the steps of processing.

Two articles deal with aspects of computerization: L. R. WINGATE balances the advantages of computerizing data versus the work and time necessary to enter data of specimen records that have already been placed in a traditional, manual catalogue before computerization (*retroactive data capture*). R. D. OWEN emphasizes the possible cooperation (consortium development) between different museums with the help of computers.

J. MEESTER deals with the necessity of retaining specimens identified by a recognized authority for the purpose of forming reference collections (voucher specimens). The contribution to nature conservation in South Africa of research collections of natural history museums and their curators is discussed by I. L. RAUTENBACH and E. M. HERHOLDT.

This interesting book is certainly of value to all those persons that deal with the management of biological collections.

P. LANGER, Gießen

GENOWAYS, H. H. (ed.): **Current mammalogy.** Vol. 2. New York and London: Plenum Press 1990. 577 pp., Abb., Tab. US $ 85,–. ISBN 0-306-43304-4

Der Band enthält zwölf Übersichtsreferate aus verschiedenen Gebieten der Säugetierkunde: WILSON und EISENBERG behandeln „Entstehung und Anwendung der Mammalogie in Nordamerika“, spannen allerdings ihre Betrachtung so weit, daß für speziellere Ausführungen allzu wenig Raum bleibt. MCBEE und BICKHAM bieten einen außerordentlich inhaltsreichen Überblick über Säugetiere als Bioindikatoren. So findet man hier nicht nur viele Angaben über die in verschiedenen Säugetierarten gemessenen mittleren Konzentrationen von Umweltgiften, sondern auch deren Toxizität und Wirkungsweise. Über die Bekämpfung von Schadnagern in Kokos-Plantagen auf den Philippinen (fast ausschließlich *Rattus rattus* und *R. exulans*) berichtet P. MILAN. Der Name "rice field rat" sollte allerdings nicht für die Hausratte, sondern für *Rattus argentiventer* verwendet werden. Die Populationsdynamik von Schneeschuhhasen *(Lepus americanus)* ist ein viel zitiertes Beispiel für Räuber-Beute-Beziehungen. L. B. KEITH findet, daß im Norden tatsächlich zehnjährige Häufigkeitszyklen bestehen, die recht gut synchronisiert sind und offensichtlich durch Nahrungsverknappung im Winter mit verringerter Geburtenrate im folgenden Sommer sowie verstärktem Feinddruck zustande kommen. Inzwischen ist durch Sendermarkierung gezeigt worden, daß für die hohe Mortalität der Junghasen nach Dichtemaxima fast ausschließlich Freßfeinde verantwortlich sind. Erdbaue von Säugetieren, ihre Vor- und Nachteile, Wühltechniken, morphologische und physiologische Anpassungen sind ein reizvolles Thema, das hier allerdings von REICHMANN und SMITH allzu kursorisch behandelt wird. So reichen nicht nur bei einigen Bathyergiden die Schneidezähne mit ihren Wurzeln bis hinter die Molaren – im Unterkiefer gilt das für sehr viele Nager. Unklar ist, warum zwischen "sensitive hairs" und "sensitive vibrissae" unterschieden wird. Zur Maulwurfschnauze werden nur „sensory papillae“, nicht aber Eimersche Organe erwähnt. Die Arbeiten von MORLOK (1983: Grabanpassungen bei subterranen Nagern), KLEIN (1972) und WITTE (verschiedene: Biologie Maulwurf) sind nicht zitiert. Die Verteilung zwischen Ruhe, Aktivität und Zeit der Nahrungsaufnahme in Abhängigkeit von Körpergröße, Nahrungsart und anderen Parametern untersuchen BUNNELL und HARESTAD. Die neuesten Befunde über Hypophysenvorderlappen und endokrinen Hypothalamus der Säugetiere faßt E. L. P. ANTHONY zusammen. COPPINGER und SMITH entwickeln und begründen eine eigene Hypothese über die Verhaltensontogenese und das Spielverhalten bei Säugetieren. Danach sind Neugeborene und Adulte unterschiedlich adaptierte Lebensformen, das Verhaltensrepertoire der Adulten ersetzt das der Neonaten. Der Übergang zwischen beiden Formen ist mit einer Metamorphose zu vergleichen, während der stückweise die ursprünglichen Bewegungskoordinationen und

Motivationen verschwinden, während die Adultelemente ebenso stückweise auftreten. Die variable und unterschiedliche Kombination erscheint als Spielverhalten. STUCKY analysiert die Evolution der Landsäugetiere im Kenozoikum Nordamerikas mit dem Ergebnis, daß die Diversität hier seit dem mittleren Paleozän konstant geblieben ist. Im Alttertiär waren lokale Faunen zwar unterschiedlicher als später, stimmten dafür aber zwischen verschiedenen Orten besser überein. Dies kann mit einem kühleren und trockeneren Klima seit dem Ende des Eozäns erklärt werden. Die Phylogenie der Marsupialier revidieren MARSCHALL, CASE und WOODBURNE, gestützt auf die Kenntnis der rezenten und fossilen Formen, die sie bis zur Familie einer kladistischen Analyse unterziehen – eine außerordentlich kenntnisreiche, konzentrierte und durchdachte Arbeit! NOVACEK präsentiert ein Kladogramm der Eutheria, das neben einem „Busch" von neun Stammeslinien, die vom gleichen Punkt entspringen, folgende speziellere Aussagen enthält, die er jeweils auch mit Synapomorphien begründet: Xenarthren und Pholidoten sind eng verwandt und bilden gemeinsam die Schwestergruppe aller übrigen Eutheria. Weiterhin faßt er die Archonta (Primaten, Scandentia, Dermoptera und Chiroptera) enger zusammen sowie Lagomorpha und Rodentia mit den Macroscelidea als Schwestergruppe. Die Paenungulata (Proboscidea+Sirenia+Hyracoidea) behält er bei. CZELUSNIAK et al., neun Autoren insgesamt, versuchen, Vergleiche von Aminosäuresequenzen und DNA taxonomisch zu werten. Tab. I informiert darüber, welche von acht Proteinen bei 86 Säugertaxa (meist Arten) inzwischen sequenziert sind. Die aufgrund dieser umfangreichen Datenbasis nach dem Prinzip der Sparsamkeit konstruierten Beziehungsschemata stimmen vielfach besser mit morphologisch begründeten Stammbäumen überein als frühere und werden zurückhaltend diskutiert.

Der Band ist sorgfältig redigiert und einheitlich, auch wenn hin und wieder noch Druckfehler vorkommen und z. B. im Kopf von Tab. I (S. 552) eine Erklärung der Buchstaben-Abkürzungen der sequenzierten Proteine fehlt. Die Mehrzahl der Beiträge ist von hoher Qualität und vermittelt den Zugang zum derzeitigen Stand eines jeweils umfangreichen, kaum noch überschaubaren Forschungsgebietes.

J. NIETHAMMER, Bonn

LABHARDT, F.: **Der Rotfuchs.** Naturgeschichte, Ökologie und Verhalten dieses erstaunlichen Jagdwildes. Mit einem Beitrag über die Fuchsbejagung von R. KRÖGER. Hamburg und Berlin: Verlag Paul Parey 1990. 158 S., 121 Abb. DM 58,–. ISBN 3-490-33812-X

FELIX LABHARDT hat zum einen eine Artmonographie zusammengestellt, die dem Anspruch auf wissenschaftliche Zuverlässigkeit, Komplexität und Verständlichkeit in einem sehr hohen Maße gerecht wird, zum anderen hat er einfach ein wunderschönes Buch über Füchse geschrieben, ausgestattet mit hervorragenden Fotografien, die zudem keine reinen „Schmuckbilder" sind, sondern vielfältige Verhaltensweisen treffend darstellen und nicht nur jeden Canidenfreund begeistern müssen!

Dieses neue Buch in der Reihe der Wildmonographien im Verlag Paul Parey ist kein Jagdbuch. Es behandelt u. a. Forschungsergebnisse zur Ernährung des Fuchses, zu seinem Verhalten in Raum – Zeit – System und enthält eine Fülle neuer Daten zum Sozialverhalten von Füchsen in unterschiedlichen Ökosystemen. Überzeugende eigene empirische Befunde werden im sorgsamen, gut recherchierten Literaturvergleich vorgestellt und diskutiert. Somit liefert LABHARDT insgesamt eine sehr solide erarbeitete, vorbildlich präsentierte Rotfuchs-Biographie. Diese richtet sich an Wildbiologen, Naturbeobachter – und an Jäger, für die insbesondere ein hoher Bedarf an Informationen zur Lebensweise dieses Raubtieres bestehen dürfte, werden doch allein in Westdeutschland etwa 170 000 Füchse pro Jahr geschossen. Möge diese umfangreiche und genaue Übersicht zu den jüngsten Forschungsergebnissen dem Jäger helfen, verbreitete Vorurteile und Halbwahrheiten über den Fuchs abzubauen, und die ökologische Bedeutung dieser faszinierenden Caniden, die er nicht selten recht unreflektiert als „Niederwildfeinde" und Konkurrenten bejagt, zu erkennen.

Das angefügte Kapitel des Fuchsjägers R. KRÖGER hätte meiner Meinung nach fehlen können, da es zur LABHARDT-Monographie weder in Aussage noch im Stil paßt. Hier werden die gängigen Formen der Fuchsjagd beschrieben, wobei es leider nicht selten an Kritik mangelt, was insbesondere für die Ausführungen über die Fallenjagd und die Baujagd gilt. Der Schlußsatz dieses Kapitels spricht dafür und für sich: „Den Fuchs scharf bejagen; das macht jägerische Freude und nutzt sowohl der Wildhege als auch Reinekes Sippe selbst".

DORIT FEDDERSEN-PETERSEN, Kiel

FREYE, H.-A.; TEMBROCK, G. (Hrsg.): **Humanethologie im Spektrum der Wissenschaften.** Nova acta Leopoldina, N. F. Nr. 273, Bd. 63. Leipzig: J. A. Barth 1990. 113 S., 17 Abb., 5 Tab. DM 48,–. ISBN 0369-5034

Im Rahmen zunehmender Spezialisierung der Wissenschaften hat die Humanbiologie als Synthese aller Grunddisziplinen, die sich mit der naturwissenschaftlichen Erforschung des *Homo sapiens* befassen, heute eine gewisse Eigenständigkeit als Grenzwissenschaft zwischen Biologie und Medizin erreicht. Die Humanethologie nimmt in ihr eine zentrale Stellung ein. Mit Recht betont H.-A. Freye in der Einleitung zu vorliegendem Band die Notwendigkeit, die Grenzen des Faches zu beachten. Die

Humanethologie ist nicht in der Lage und beabsichtigt auch nicht, das Wesen des Menschen zu erklären und verkennt nicht, daß sie nur in der Lage ist, aus einem Blickwinkel, dem naturwissenschaftlichen, sich der Problemstellung zu nähern. Das spezifisch Menschliche, Selbst- und Weltbewußtsein, Kulturfähigkeit entzieht sich weitgehend der naturwissenschaftlichen Analyse und bedarf der Teilnahme von Geistes- und Gesellschaftswissenschaften.

Ergebnisse der vergleichenden Verhaltensforschung sind aber auch für das Problem der Menschwerdung aufschlußreich, da auf diesem Weg Wurzeln menschlichen Verhaltens und Vorstufen zu diesem erkannt werden können.

Der vorliegende Band enthält 9 Beiträge führender Sachkenner aus verschiedenen Disziplinen und ist zugleich ein gutes Beispiel für die zunehmende Bedeutung interdisziplinärer Forschung. Im Einzelnen seien folgende Beiträge hervorgehoben.

G. Vollmer bringt eine knappe und klare Übersicht über Grundfragen der evolutionären Erkenntnistheorie als Basis synthetischen Denkens in der Biologie. Eine sinnvolle Ausweitung dieses Ansatzes auf weitere Gebiete und grundsätzliche Fragen der Abgrenzung werden erörtert. Soziale Kognition in nichtmenschlichen Primatengesellschaften und deren primäre Bedeutung vor Erreichen des Werkzeuggebrauches sind Thema von Ch. Vogel. Weitere Beiträge behandeln die Evolution kognitiver Prozesse (Klix). Es folgt ein Beitrag über Bedeutung hormonal abhängiger Prozesse in der Hirnentwicklung (G. Dörner). Verhaltensprozesse im Bereich der Wechselwirkung von Interaktionen zwischen Organismus und Umwelt während der perinatalen Lebensphase behandelt G. Tembrock. Zur Frage nach der Hirnentwicklung und dem Verhalten in der menschlichen Ontogenese berichtet G. Wolf, während P. Propping die Abhängigkeit der Hirnfunktion von der genetischen Variabilität behandelt. Eibl-Eibesfeld untersucht pathologische Verhaltensweisen beim Menschen aus der Sicht des vergleichenden Ethologen. Die Schrift bietet eine nützliche Übersicht über Entwicklungen und Fortschritte auf dem Gebiet der Humanethologie durch kompetente Autoren und kann zur Lektüre empfohlen werden. D. Starck, Frankfurt/M.

Emmons, Luise H.; Feer, F.: **Neotropical Rainforest Mammals.** A Field Guide. Chicago and London: The University of Chicago Press 1990. 281 S., 11 Abb., 29 Farbtafeln, 7 Schwarzweißtafeln, 184 Verbreitungskarten. Kart. US $ 51.75. ISBN 0-226-20718-8

Das Buch behandelt die Säugetiere der unterhalb von 1000 m NN gelegenen Regenwälder Mittel- und Südamerikas in der für moderne Feldführer üblichen Weise: Englischer und wissenschaftlicher Name, Merkmale mit Spannweiten der Körpermaße und Gewichte, innerartliche Variabilität, Verwechselungsmöglichkeiten, Lautäußerungen, Lebensweise, Verbreitung, Gefährdungsstatus und eventuell 1–2 Literaturhinweise. Im Anhang finden sich Bestimmungsschlüssel für die Familien und Gattungen, Erläuterungen zu Taxonomie, Verbreitung und Schutz, Abbildungen von Fährten einiger größerer Arten und eine komplette Artenliste, durch Fett- und Normaldruck gegliedert in echte Regenwaldarten und solche, die nur vom Rande her hineinreichen. Im allgemeinen werden alle Arten, bei den Fledermäusen und myomorphen Nagern jedoch nur die Gattungen behandelt, und für diese Gruppen ist die komplette Artenliste im Anhang als Ergänzung besonders wichtig. Der Text stammt von Luise H. Emmons, die Abbildungen sind von F. Feer und umfassen für alle behandelten Einheiten Habitusbilder, bei den Fledermäusen meist nur Kopfporträts und häufiger auch die Gestalt der Schwanzflughaut. Die Autoren haben sich vor allem auf die neueste Literatur und die Sammlungen großer amerikanischer und europäischer Museen gestützt. Erstmals wird mit diesem Taschenführer ein großer Teil Süd- und Mittelamerikas erfaßt, in dem etwa 500 Säugetier-Arten vorkommen. Die Farbbilder wirken zwar ziemlich grob, dürften aber für den Zweck des Buches ausreichen. Gebißformeln finden sich nur in den Familienbeschreibungen. Merkmale, die nicht äußerlich am lebenden Tier feststellbar sind, werden sonst nicht erwähnt. Qualität und Grenzen des Führers sind für einen Europäer am besten zu beurteilen, wenn er Artbeschreibungen wie die für Haus- und Wanderratte vergleicht. Neben überwiegend zutreffenden Angaben fallen hier allzu subjektive Bemerkungen auf wie bei Lautäußerungen (Hausratte nagt und läuft geräuschvoll, Wanderratte quiekt und kämpft) oder Wanderratten sind „very large, robust, ugly rats". Der Wert des Größenunterschiedes zur Unterscheidung der Arten ist überbetont, daß Hausratten außerhalb der Neotropis Regenwaldbewohner sind, dürfte nicht stimmen.

Die Beschränkung auf Gattungen in einigen artenreichen Familien ist bedauerlich, ebenso das allzu kurze allgemeine Literaturverzeichnis S. 206, in dem z. B. Eisenberg (1989), Cabrera und Yepes (1960), Husson (1978) oder Mares und Genoways (1982) fehlen. Demgegenüber ist aber hervorzuheben, daß die knappe Behandlung eines so umfangreichen Stoffes, die Orientierung in der vielfach noch unklaren Taxonomie, die Sammlung allein der zahlreichen Verbreitungskarten und Maße eine bewundernswerte Leistung darstellt.

Dies Buch dürfte für eine erste Orientierung bei Begegnungen mit Säugetieren in neotropischen Regenwäldern von großem Nutzen sein. J. Niethammer, Bonn

Fortsetzung von der 1. Umschlagseite

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers, PO Box 1815, New York, NY 10156-0610, USA. Phone (212) 679–0782, Telefax (212) 213–3798.

Erscheinungsweise und Bezugspreis 1992: 6 Hefte bilden einen Band. Jahresabonnement Inland: 358,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 351,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 358,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde“ erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 57 (1992) 3, 129–192

Grundlagen der Röntgenologie in der Veterinärmedizin

2., überarbeitete und erweiterte Auflage von Sidney W. Douglas M. A., MRCVS, DVR; Michael E. Herrtage M. A., BVSC, MRCVS, DVR; Hamar D. Williamson M. A., BA, DCR, Department of Clinical Veterinary Medicine, University of Cambridge

Aus dem Englischen übertragen und bearbeitet von Dr. Beate Münzer, unter Mitarbeit von Prof. Dr. Klaus Hartung, beide Klinische Radiologie an der Klinik für Pferdekrankheiten, Allgemeine Chirurgie und Radiologie, Freie Universität Berlin

1991. 204 Seiten mit 166 Abbildungen und 10 Tabellen. 24 x 16,5 cm.
Kart. DM 88,– ISBN 3-489-51916-7

Die rasche Weiterentwicklung der Röntgenologie in der Veterinärmedizin machte eine gründliche Überarbeitung dieses Buches für die zweite Auflage erforderlich, die in allen Kapiteln ihren Niederschlag gefunden hat. Die für die praktische Anwendung der Röntgenstrahlen unerläßlichen physikalischen Grundlagen sind im Teil 1 intensiver aufgeführt und die folgenden Kapitel über Röntgengeräte, Zusatzgeräte und Filmentwicklungstechniken auf den neuesten Stand gebracht worden. Dies gilt ebenso für den Abschnitt über Strahlenschutz, der aufgrund neuerlassener Verordnungen nun dem aktuellen Stand der notwendigen und gesetzlich erfaßten Strahlenschutzmaßnahmen entspricht.

Das Buch wendet sich an die Studierenden und an die praktizierenden Tierärzte, um ihre theoretischen und praktischen Kenntnisse in der Radiologie zu festigen und einen sicheren und effizienten Umgang mit den Röntgenstrahlen zu gewährleisten. Darüber hinaus werden mit dieser Neuauflage auch die röntgentechnischen Assistenten angesprochen, die eine wichtige Stütze in der veterinärmedizinischen Röntgenologie darstellen, sowie die Praktiker, die ein spezielles Interesse an röntgenologischen Untersuchungsmethoden haben.



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ZEITSCHRIFT FÜR SÄUGETIERKUNDE

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

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Z. Säugetierkunde 57 (1992) 193–200

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Regionale und saisonale Unterschiede in der Nahrungszusammensetzung des Großen Mausohrs *Myotis myotis* (Chiroptera, Vespertilionidae) in der Schweiz

Von M. Graf, H.-P. B. Stutz und V. Ziswiler

Zoologisches Museum der Universität Zürich, Schweiz

Eingang des Ms. 10. 12. 1991
Annahme des Ms. 17. 2. 1992

Abstract

Regional and seasonal differences of the food composition of the Mouse-eared bat Myotis myotis (Chiroptera, Vespertilionidae) in Switzerland

Studied the contents of the feces of *Myotis myotis*, collected in 14 nursery roosts in the central, northern and eastern parts of Switzerland regionally and seasonally. The taxa, established with literature and collection-references were quantified with the method of Korschgen (1971). In all colonies Carabidae were the basic food. Other important prey were Orthoptera (Acrididae, *Gryllotalpa gryllotalpa*), Diptera (Tipulidae) and Arachnida. The seasonal variation of the diet of *Myotis myotis* seemed to be correlated with the seasonal prey availability. A selection of large prey (> 10 mm) was supposed. A cluster analysis revealed 3 regional groups of nursery roosts which were classed according to landscape and intensity of agricultural land use. The results were discussed with respect to possible habitat change.

Einleitung

Viele insektivore Fledermausarten verhalten sich in ihrer Ernährung opportunistisch (Fenton und Morris 1976). Hinweise für eine allfällige selektive Ernährung können entweder durch den quantitativen Vergleich von Nahrungszusammensetzung und Beuteangebot am selben Ort oder durch den Vergleich der Nahrungszusammensetzung in verschiedenen Landschaftsräumen gewonnen werden. Für *M. myotis* wird einerseits eine Spezialisierung auf bodenlebende Insekten und andererseits eine selektive Bevorzugung großer Beutetiere vermutet (Kolb 1958; Bauerova 1978; Ackermann 1984).

Wochenstubenquartiere von *M. myotis* verteilen sich in der Schweiz auf die Landschaftsregionen Jura, Mittelland, Voralpen und Alpen (Stutz und Haffner 1984a). Damit bietet sich die Möglichkeit, durch einen Vergleich der Nahrungszusammensetzung in den verschiedenen Regionen ein differenzierteres Bild über die Ernährung von *M. myotis* zu gewinnen. Von speziellem Interesse ist dabei das Ausmaß der Präferenz für waldbewohnende Carabidae, die bei allen bisherigen Arbeiten festgestellt wurde (Kolb 1958; Bauerova 1978; Ackermann 1984; Pont und Moulin 1985; Gebhard und Hirschi 1985).

Material und Methode

Aus 14 Wochenstubenquartieren von *M. myotis* wurden Kotproben (n = 102 Proben) analysiert. Hierfür wurde der frisch angefallene Kot unter dem Haupthangplatz in 4-Wochen-Intervallen vom 10. 4. 1988 bis 23. 10. 1988 gesammelt. Pro Kolonie ergab dies maximal acht Proben, von denen je 20 Kotballen einzeln nach taxonomisch auswertbaren Beuteüberresten untersucht wurden. Diese unverdauten Beuteteile wurden anhand von Literaturangaben und mit Hilfe von Vergleichssammlungen einzelnen Invertebratentaxa zugeordnet.

Die Quantifizierung der qualitativ erfaßbaren Beutekategorien wurde nach Korschgen (1971)

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durchgeführt: die Anzahl Kotballen, in denen eine Beutekategorie nachgewiesen wurde, ergab die Frequenz F, mit einem Wertebereich von 0 bis 20.

Für die Gruppierung der Wochenstubenquartiere aufgrund der ermittelten Beutefrequenzen wurde eine Cluster-Analyse mit dem Programmpaket MULVA-4 Version 1.02 (Wildi und Orloci 1988) durchgeführt. Aus diesem Paket wurden die Programme INIT, CLTR und TABS verwendet. Die Klassenwerte wurden nicht transformiert. Für die Ähnlichkeitsmatrizen wurde das Kontingenzmaß nach Van den Maarel verwendet. Die Cluster-Analyse wurde mit einem minimum-variance-clustering durchgeführt (Wildi 1986). Die Beutefrequenzen wurden in fünf Größenklassen (F = 0–2,4, F = 2,5–7,4; F = 7,5–12,4; F = 12,5–17,4; F = 17,5–20) eingeteilt und für jedes Wochenstubenquartier die acht monatlichen Proben in den drei Gruppen Frühling (März–Mai), Sommer (Juni, Juli) und Herbst (Aug.–Sept.) zusammengefaßt.

Ergebnisse

Aufgrund der festgestellten Häufigkeiten können Coleoptera, Orthoptera, Diptera und Arachnida als wichtigste Beutekategorien bezeichnet werden (Abb. 1). Die Ordnung Coleoptera wurde in allen monatlichen Proben am häufigsten nachgewiesen (Abb. 2). Der größte Anteil der Nachweise entfällt dabei auf die Familie Carabidae (Abb. 3). Bei der Familie Scarabaeidae zeigt sich, daß Bruchstücke von *Melolontha melolontha/hippocastani*

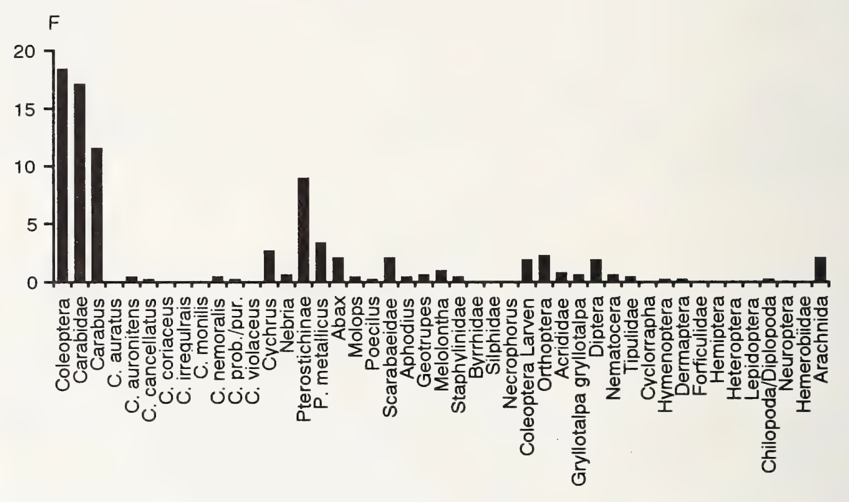


Abb. 1. Jahresmittelwerte der Nachweishäufigkeiten (F) der verschiedenen Beutekategorien im Kot der untersuchten Wochenstubenquartiere von *M. myotis*. Die Daten aus sämtlichen Wochenstubenquartieren wurden zusammengefaßt

nur im April, Mai und Juni festgestellt werden konnten (Abb. 3). Die Scarabaeidae-Nachweise in der zweiten Jahreshälfte entfallen demgegenüber mehrheitlich auf die Gattungen *Aphodius* und *Geotrupes*. Die Ordnung Orthoptera konnte am häufigsten im August, September und Oktober nachgewiesen werden (Abb. 2). Bei den Nachweisen im Mai und Juni handelt es sich fast ausschließlich um Bruchstücke von *Gryllotalpa gryllotalpa*. Die hohen Frequenzen im August, September und Oktober sind dagegen mehrheitlich in Nachweisen von Acrididae begründet (Abb. 3). Die Frequenzen von Diptera weisen zwei Maxima auf. Das erste ist im Mai und Juni und das zweite im August und September zu verzeichnen (Abb. 2). Die höchsten Frequenzen für die Klasse Arachnida konnten im Frühling und Herbst festgestellt werden (Abb. 2).

Die Gruppierung der Wochenstubenquartiere mittels einer Cluster-Analyse aufgrund der Beutefrequenzen ergab drei Hauptgruppen (Abb. 4, Tab. 1). Diese zeigen eine

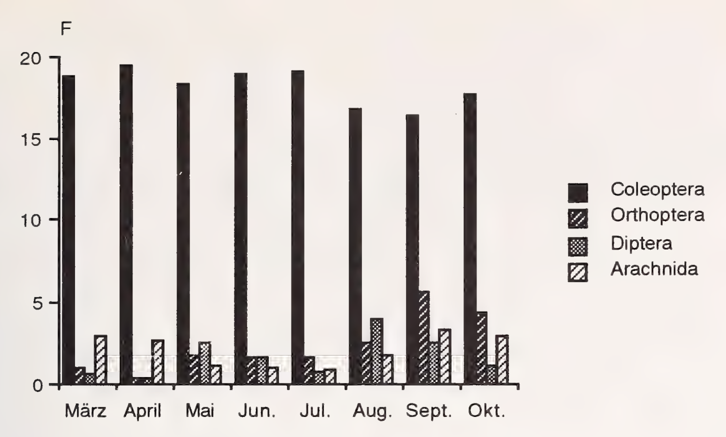


Abb. 2. Mittlere monatliche Nachweishäufigkeiten (F) von Coleoptera, Orthoptera, Diptera und Arachnida. Die Daten aus sämtlichen Wochenstubenquartieren wurden zusammengefaßt

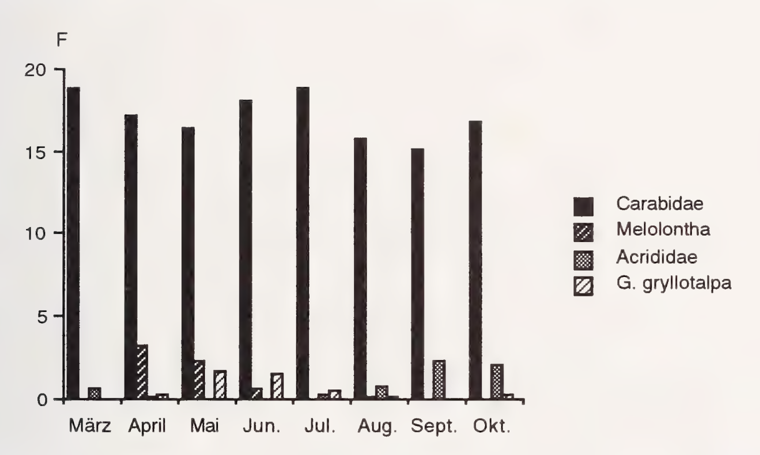


Abb. 3. Mittlere monatliche Nachweishäufigkeiten (F) von Carabidae, *Melolontha*, Acrididae und *Gryllotalpa gryllotalpa*. Daten aus sämtlichen Wochenstubenquartieren wurden zusammengefaßt

Übereinstimmung mit der geographischen Gliederung des Untersuchungsgebietes und mit den landwirtschaftlichen Eignungsklassen (Bundesamt für Landwirtschaft 1986) (Abb. 5).

Die für die Gruppe 1 charakteristische Nahrungszusammensetzung zeichnet sich durch sehr hohe Carabidae-Frequenzen in allen Proben aus (Abb. 5, 6). Mit einer Ausnahme (Wochenstubenquartier in Sachseln, Sa) befinden sich alle Wochenstubenquartiere der Gruppe 1 im Mittelland sowie in der landwirtschaftlichen Eignungsklasse „sehr günstig".

Die Gruppe 2 umfaßt die Wochenstubenquartiere, deren Nahrungszusammensetzung sich durch tiefere Carabidae-Frequenzen bzw. höhere Frequenzen von Acrididae, *Gryllotalpa gryllotalpa* und Diptera (Tipulidae) auszeichnen (Abb. 5, 6). Diese Quartiere liegen einerseits im Übergangsbereich zwischen Mittelland und Alpen (in der Folge als Voralpen bezeichnet) und andererseits in der landwirtschaftlichen Eignungsklasse „günstig" oder in den Grenzgebieten der Eignungsklasse „bedingt geeignet".

Das einzige Wochenstubenquartier der Gruppe 3 zeichnet sich durch die tiefsten Carabidae-Frequenzen sowie durch hohe Frequenzen für Acrididae und *Melolontha melolontha/hippocastani* aus (Abb. 5, 6). Dieses Quartier liegt in den Alpen auf 1016 m ü. M. in der landwirtschaftlichen Eignungsklasse „bedingt geeignet".

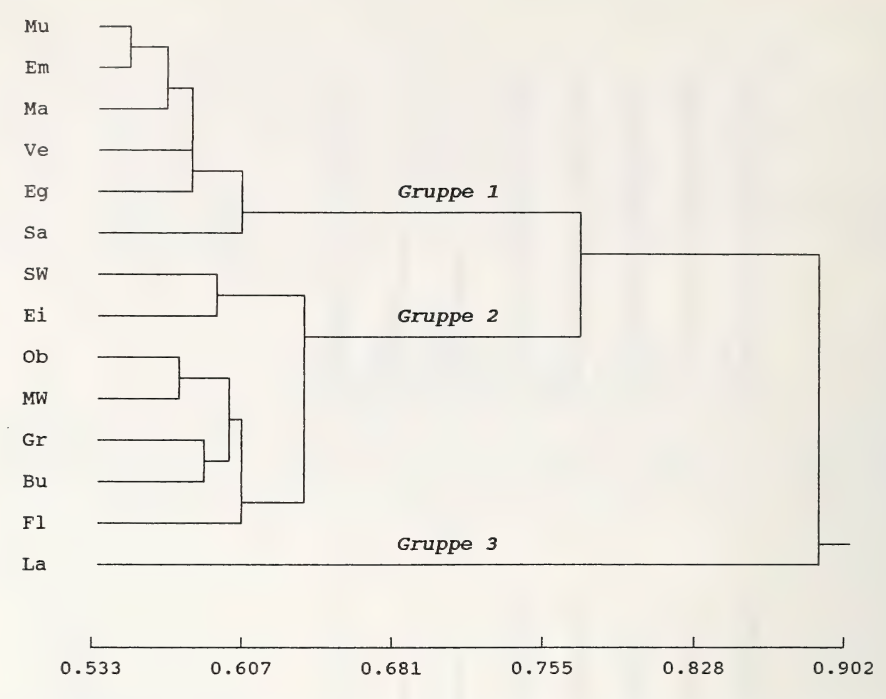


Abb. 4. Minimum-Variance-Dendrogramm der untersuchten Wochenstubenkolonien aufgrund der Beutefrequenzen. Ähnlichkeitsmaß: Van den Maarel Koeffizient (nach Wildi und Orloci 1988)

Diskussion

Mit der in der vorliegenden Arbeit verwendeten Methode der Kotanalyse sind Aussagen über die Ernährung möglich (Kunz und Whiteaker 1983). Die Wahrscheinlichkeit der taxonomischen Zuordnung der unverdauten Beuteüberreste ist jedoch von der taxonomischen Relevanz der im Kot aufgefundenen Körperteile abhängig. Die hier verwendete Methode der Frequenzerfassung hat den Vorteil, daß keine Schätzungen vorgenommen und keine unbestimmbaren Bruchstücke zugeordnet werden müssen. Die Stichprobengröße von 20 Kotballen kann aufgrund eigener Erfahrungen (Graf 1990) und aufgrund der Angaben von Pont und Moulin (1985) als ausreichend angesehen werden. Die Zuordnung des Wochenstubenquartieres in Sachseln, Sa durch die Cluster-Analyse ist vermutlich mit methodischen Fehlern behaftet. So fehlt die Probe September, die allgemein diagnostischen Charakter für die Gruppierung aufweist (Tab. 1). Deshalb wird die Zuordnung zur Gruppe 1 als nicht stichhaltig erachtet.

Grundsätzlich kann festgehalten werden, daß Carabidae in allen 14 Wochenstubenquartieren während des Sommerhalbjahres 1988 den Hauptbestandteil der Nahrung von *M. myotis* ausmachten. Die saisonalen Unterschiede der Nachweishäufigkeiten weisen zusätzlich aber auf eine Beeinflussung der Nahrungszusammensetzung durch ein saisonal variables Beuteangebot hin. Am offensichtlichsten ist dieser Zusammenhang bei *Melolontha melolontha/hippocastani*, die während ihrer Flugzeit im Mai und Juni auch am häufigsten im Kot nachgewiesen wurden. Im weiteren wurde die hauptsächlich unterirdisch lebende *Gryllotalpa gryllotalpa* fast ausschließlich zur Zeit ihrer Paarungsaktivität im Mai und Juni gefressen, wenn diese sich vermehrt an der Oberfläche aufhält. Tipulidae wurden hauptsächlich im Mai sowie im August und September gefressen. Im Gegensatz zu

Klassenwerte der für die Cluster-Analyse verwendeten Beutekategorien

1: F = 0–2,4; 2: F = 2,5–7,4; 3: F = 7,5–12,4; 4: F = 12,5–17,4; 5: F = 17,5–20
Frühling: März, April, Mai; Sommer: Juni, Juli; Herbst: August, September, Oktober

	Gruppe1						Gruppe 2							Gruppe3
Beutetiergruppe	Mu	Em	Ma	Ve	Eg	Sa	St	Ei	Ob	Ml	Gr	Bu	Fl	La
Heteroptera Sommer													1	
Neuroptera Frühling		1											1	
Acrididae Frühling								1					1	
Heteroptera Frühling										1			1	
Heteroptera Herbst	1													1
Neuroptera Herbst														1
Acrididae Sommer											1		1	
Hymenoptera Frühling		1												1
Chilo-/Diplopoda Sommer	1	1			1									
Dermaptera Frühling	1	1			1									
Coleoptera Larven Herbst	1	1		1	1			1			1		1	1
Arachnida Sommer	1			2	1	1			1		1	1	1	1
Coleoptera Larven Sommer	1	1	1		2	1			1				1	
Hymenoptera Sommer	1	1	1			1							1	1
Chilo-/Diplopoda Frühling					1	1							1	
Gryllotalpidae Herbst						1				1				
Chilo-/Diplopoda Herbst	1					1		1		1	1		1	
Staphylinidae Herbst	1	1	1	1		1	1	1	1	1				1
Staphylinidae Frühling		1	1			1	1	1	1					
Gryllotalpidae Sommer	1				1	2	2	1		1	1	1		
Gryllotalpidae Frühling						1	2		1	2		1	1	
Silphidae Sommer							1							
Silphidae Frühling	1								1					
Lepidoptera Herbst					1							1		
Staphylinidae Sommer		1	1					1		1				
Lepidoptera Sommer			1								1			
Byrrhidae Frühling								1			1	1		
Carabidae Sommer	5	5	5	5	5	4	5	4	5	5	5	5	5	3
Carabidae Frühling	5	5	5	5	5	4	4	4	4	4	5	5	5	2
Carabidae Herbst	5	5	5	5	5	5	4	3	4	4	4	3	4	2
Diptera Sommer	1	1	2	1	1	1	1	1	1		2		1	1
Diptera Frühling	1	1	1	1	1	1	2	2	1	1	2	1	1	1
Coleoptera Larven Frühling	3	2	3	3	2	2	2	1	1	2	2	2	1	1
Arachnida Frühling	2	1	1	2	2	2	1	1	1	1	2	2	1	1
Scarabaeidae Herbst	2	1	1	1	1	1		1	2	2	2	2	1	1
Arachnida Herbst	2	2	2	1	2	1	1	1	2	1	2	1	1	
Diptera Herbst	1	1	1		1	1	2	2	2	2	2	3	2	1
Acrididae Herbst					1		2	1	1	1	1	1	1	3
Dermaptera Herbst					1		1	1			1		1	2
Hymenoptera Herbst			1		1		1				1		1	1
Scarabaeidae Sommer			1			1			1		1	1	1	2
Scarabaeidae Frühling	1	1		1		1	1	1	2	2	2	1	1	4

den vorgängig erwähnten Arten sind Tipulidae jedoch im ganzen Sommerhalbjahr vorhanden (Dufour 1986), doch scheinen sie im Mai, August und September für *M. myotis* optimal verfügbar zu sein. Bemerkenswert ist, daß die für die Tipulidae-Männchen typischen Büschelfühler nie festgestellt werden konnten, obwohl diese kaum häufiger abgebissen werden dürften als die regelmäßig nachgewiesenen Fühler der Weibchen. Zudem traten Bruchstücke von Tipulidae im Kot sehr häufig zusammen mit einer großen Zahl von Eiern auf, die große Ähnlichkeit mit Tipulidae-Eiern aufweisen. Vermutlich handelt es sich beim größten Teil der nachgewiesenen Tipulidae um Weibchen, die sich während der Eiablage in Bodennähe aufhielten. Daher ist anzunehmen, daß Tipulidae wegen des speziellen Verhaltens der Weibchen während der Eiablage gefressen wurden. Ein weiterer Hinweis für das Ablesen der Beutetiere von einem Substrat läßt sich ebenfalls von den Nachweishäufigkeiten der Arachnida ableiten. Da bei dieser Beutekategorie eine genauere Bestimmung nicht möglich war, ist eine eingehendere Diskussion jedoch nicht möglich.



Abb. 5. Das Untersuchungsgebiet mit den landwirtschaftlichen Eignungsklassen (Raster) und den mittels der Cluster-Analyse gruppierten Wochenstubenquartieren (Punktsymbole). Dreiecke = Gruppe 1; Kreise = Gruppe 2; Quadrate = Gruppe 3. Helles Raster: landwirtschaftliche Eignungsklasse „günstig"; mittleres Raster: landwirtschaftliche Eignungsklasse „sehr günstig"; dunkles Raster: landwirtschaftliche Eignungsklasse „bedingt geeignet"

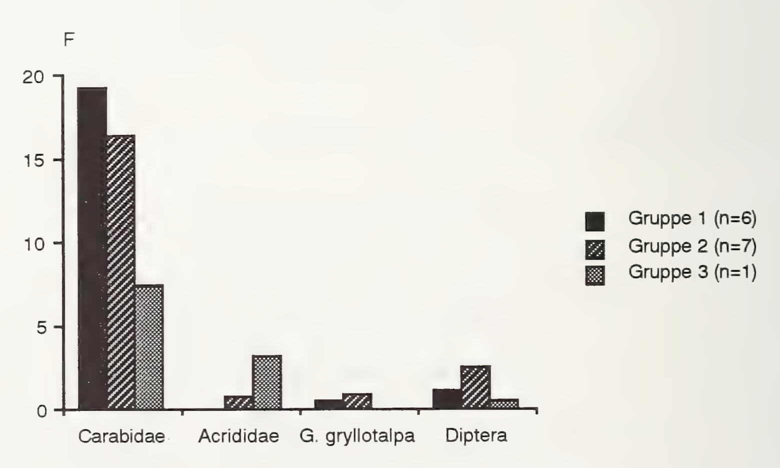


Abb. 6. Jahresmittelwert der Nachweishäufigkeiten der wichtigsten Beutekategorien in den drei durch die Cluster-Analyse gebildeten Gruppen der Wochenstubenquartiere

Die Nahrungszusammensetzung scheint aber nicht nur durch die saisonale Verfügbarkeit der verschiedenen Beutetiergruppen beeinflußt zu werden, sondern auch durch die Beutegröße. So zeigen die in der Literatur (Freude et al. 1969, 1976; Chinery 1984; Bellmann 1985) angegebenen Körpergrößen für alle regelmäßig nachgewiesenen Beutetiere, daß diese zu den mittelgroßen bis großen Arthropoden ($\geq$ 10 mm) gehören. *M. myotis* scheint demnach selektiv große Beutetiere zu fressen, was die Vermutung von Bauerova (1978) und Ackermann (1985) bestätigt.

Die regionale Gruppierung der Wochenstubenquartiere durch die Cluster-Analyse kommt in erster Linie durch die unterschiedlichen Carabidae-Frequenzen zustande (Tab. 1). Die meisten nachgewiesenen Carabidae sind waldbewohnende Arten, während die bei gleichzeitig geringeren Carabidae-Frequenzen auftretenden weiteren bedeutenden Beutekategorien weniger oder gar nicht in Wäldern leben. Zur Deutung dieser regionalen Unterschiede bieten sich folgende Erklärungsmöglichkeiten an:

Unter der Voraussetzung, daß *M. myotis* nach Möglichkeit in Wäldern jagt, könnte die Verfügbarkeit der Carabidae für *M. myotis* in den Voralpen und Alpen bereits zu gering sein, weshalb Insekten vermehrt auch außerhalb des Waldes erbeutet werden müßten. Entweder wäre in diesen Gebieten die Dichte der Carabidae effektiv geringer, oder die Auffindbarkeit der Carabidae wäre für *M. myotis* schlechter.

Die Übereinstimmung der Gruppierung der Kolonien mit den landwirtschaftlichen Eignungsklassen, welche ihrerseits als Intensitätsmaß für die landwirtschaftliche Nutzung dienen, führt zu einer zweiten Hypothese. Diese basiert darauf, daß *M. myotis* als vergleichsweise große Fledermausart auf das Fressen von großen Insekten spezialisiert ist. Das Angebot an Großinsekten in offenen Habitaten dürfte jedoch vor allem im Mittelland durch die erfolgten Landschaftsveränderungen stark zurückgegangen sein. Dies hätte in der Folge zu einer Verlagerung zum hauptsächlichen Beuteerwerb von waldlebenden Insekten (v. a. Carabidae) geführt. Unter diesem Gesichtspunkt müßte die ausgeprägte Nutzung von Wäldern als Jagdhabitate (Audet 1990; Rudolph 1989; Güttinger mdl. Mitt.) jedoch als sekundär eingestuft werden.

In diesem Zusammenhang ist auch der Vergleich mit *Rhinolophus hipposideros* sehr aufschlußreich. Ähnlich *M. myotis* erlitt auch diese Fledermausart in der Schweiz in den letzten Jahrzehnten einen starken Bestandesrückgang. Während *R. hipposideros* jedoch gleichzeitig einen Arealverlust im Schweizer Mittelland erfuhr (Stutz und Haffner 1984b), konnte sich *M. myotis* hier zumindest in Restbeständen halten. Da beide Arten im Mittelland vermutlich in ähnlichem Ausmaß auf Dachstockquartiere angewiesen sind, dürften Ursachen für die oben aufgezeigten Unterschiede außerhalb der Tagesschlafverstecke zu suchen sein. Hier bieten sich die unterschiedliche Ernährung und die unterschiedlichen Jagdhabitate als beste Erklärungsmöglichkeiten an. Aufgrund von Nahrungsanalysen (Beck et al. 1989; Jones und Rayner 1989) kann für *R. hipposideros* eine stärkere Bindung an eine kleinräumig strukturierte Kulturlandschaft außerhalb des Waldes angenommen werden. Somit hätte die hauptsächlich durch die zunehmende Intensivierung in der Landwirtschaft verursachte Ausräumung der offenen Landschaft *R. hipposideros* in stärkerem Maße betroffen als *M. myotis*. Diese hat im Mittelland außerhalb des Waldes allenfalls einen Teil ihres Beutespektrums verloren, verfügt aber noch immer über eine gesicherte Nahrungsgrundlage im Wald.

Danksagung

Für die wissenschaftliche Unterstützung danken wir Dr. M. Haffner. Bei Prof. Dr. W. Sauter, Dr. G. Bächli und A. Beck bedanken wir uns für die Unterstützung bei der taxonomischen Zuordnung der unverdauten Beuteteile. Im weiteren danken wir R. Güttinger für die vielen anregenden Diskussionen und allen Quartierbetreuern für die Mithilfe bei der Materialbeschaffung. Die vorliegende Arbeit entstand innerhalb des Forschungsprogrammes des dritten Autors, das vom Schweizerischen Nationalfond unterstützt wurde.

Zusammenfassung

Ein Vergleich der Resultate von Kotanalysen in 14 Wochenstubenquartieren von *M. myotis* ergab, daß Carabidae in allen Regionen des Untersuchungsgebietes den Hauptbestandteil der Nahrung bildeten. Es zeigte sich eine Ausrichtung nach dem saisonalen Angebot, wobei allgemein selektiv mittelgroße und große Beutetiere (> 10 mm) bevorzugt wurden. *M. myotis* verhält sich somit bei der Wahl der Beutetaxa opportunistisch, bei der Wahl der Beutegröße hingegen selektiv.

Die mittels einer Cluster-Analyse festgestellte regionalen Unterschiede der Nachweishäufigkeiten können verschieden gedeutet werden.

Entweder führte eine allgemein geringere Verfügbarkeit der Carabidae in den Voralpen und Alpen zur vermehrten Nutzung anderer Beutekategorien, oder das Fressen waldlebender Carabidae im Schweizer Mittelland ist als Folge eines nicht mehr genügenden Angebotes an Großinsekten außerhalb des Waldes anzusehen. Dies würde bedeuten, daß die Wahl geeigneter Jagdhabitate in starkem Maße durch das Beuteangebot beeinflußt wird.

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Nachweis des Baummarders, *Martes martes,* in der neolithischen Ufersiedlung von Twann (Kanton Bern, Schweiz) sowie Anmerkungen zur osteometrischen Unterscheidung von *Martes martes* und *M. foina*

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Eingang des Ms. 25. 9. 1991
Annahme des Ms. 25. 2. 1992

Abstract

Neolithic remains of the Pine marten, Martes martes from Twann (Switzerland) and osteometrical methods to distinguish M. martes from M. foina

Studied the bones representing the genus *Martes* and compared them with those of modern individuals. From the 200 000 bone fragments excavated at Twann, on the shore of Lake Biel, 149 belong to *Martes martes.* They represent 25 individuals, making up 1.7 % of all the wild animals from this site. These pine martens were probably used for food as well as for their fur. Osteometrical methods to distinguish *M. martes* from *M. foina* and also the sexes of each species are discussed.

Einleitung

Anläßlich des Nationalstraßenbaus in der Schweiz stieß man Anfang der 70er Jahre beim Bahnhof Twann am Bieler See (Jura-Südfuß) auf neolithische Siedlungsschichten. Die von 1974–1976 dauernden Ausgrabungen brachten neun Siedlungshorizonte (3838–3532 v. Chr., Suter und Schifferdecker 1986) zum Vorschein, in denen über 200 000 Knochen tierischen Ursprungs lagerten. Die knapp 80 000 nach Tierart bestimmbaren Knochenfragmente stammen zu je ungefähr der Hälfte von Haus- und von Wildtieren. Eine Gesamtauswertung der Funde erfolgte in den Jahren gleich nach der Grabung (Grundbacher und Stampfli 1977; Furger 1980; Becker 1981; Becker und Johansson 1981), wobei die Wildcarnivoren späteren Detailuntersuchungen vorbehalten blieben (Grundbacher 1990; Grundbacher et al. 1990).

Die 149 Marderknochen, welche 0,4 % aller Wildtierknochen entsprechen, sind Gegenstand der vorliegenden Arbeit. Sie stammen von mindestens 25 Tieren (= 1,7 % aller Wildtierindividuen).

Material und Methode

Die Twanner Knochenreste

Die Marderknochen stammen meist von adulten Tieren und sind relativ gut, z. T. sogar vollständig erhalten. Nur wenige Fragmente konnten zu ganzen Knochen zusammengesetzt werden. Von den 149 der Gattung *Martes* zugeordneten Knochen waren 111 (= 74,5 %) vermeßbar (Tab. 1). Nur zwölf Knochenfunde sind angebrannt oder ganz verkohlt. Rippen und Wirbel (außer 1. und 2. Halswirbel) wurden nicht artlich bestimmt.

Das Vergleichsmaterial

Schädel und Unterkiefer rezenter Tiere stellten mir die Naturhistorischen Museen von Bern, Basel und Genf zur Verfügung. Herkunftsgebiet der mehrheitlich in diesem Jahrhundert gesammelten

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Marderschädel ist vor allem das Berner Mittelland, aber auch die übrige Schweiz und die angrenzende Haute Savoie (F). Acht Skelette von *Martes martes* aus Dänemark ergänzten das – keine Langknochen liefernde – Schweizer Vergleichsmaterial. Sämtliche subfossilen und rezenten Knochen wurden von der Autorin vermessen.

Artbestimmung

Um am ausgegrabenen Material eine sichere Artbestimmung vornehmen zu können, wurden folgende Methoden zuerst an artbekannten Vergleichsschädeln geprüft:
Distanz der Foramina mentalia in Abhängigkeit von der Gesamtlänge der Mandibel (Stampfli 1976)
Lage des hinteren Foramen mentale (Gaffrey 1953)
Verhältnis Länge Trigonid zur Gesamtlänge des M_1 (van Valkenburgh 1989).

Geschlechtsbestimmung

Mittels Clusteranalyse wurde am bekannten rezenten Material geprüft, welche Meßstrecken am Unterkiefer den deutlichsten Geschlechtsdimorphismus aufweisen (Gerasimov 1985). Die Breite des Processus condyloideus und die mit ihr korrelierte Länge der Backzahnreihe (P_2 bis M_2, da P_1 oft nicht angelegt war), erwiesen sich als brauchbare Größen, um eine Trennung unbekannten Materials in zwei Gruppen zu erreichen.

Messungen, Auswertung

Gemessen wurden die Knochen nach den Anweisungen von den Drieschs (1976) mit einer Uhrenschieblehre auf 0,1 mm genau. Bei den rezenten Exemplaren wurde jeweils nur eine Seite pro Schädel gemessen. Die Unterkiefer aus Twann wurden alle vermessen und ausgewertet, unabhängig davon, ob sie zueinander paßten oder nicht. Die Daten wurden anschließend auf einem Microcomputer mit den Statistikpaketen Systat und Sygraph bearbeitet.

Tabelle 1. **Skelettverteilung der Marderreste aus Twann**

	Vermessen	Nicht meßbar
Schädelteile	4	5
Unterkiefer	30	0
Lose Zähne	0	4
Scapula	6	1
Humerus	19	9
Ulna	6	0
Radius	8	1
Pelvis	10	1
Femur	15	10
Tibia	13	7
	111	38
	149	

Ergebnisse

Skelettverteilung

Die Verteilung der Knochen auf Hinter- und Vorderextremität (Tab. 1) ist ausgewogen. Mandibeln sind unverhältnismäßig stark vertreten. Auffällig ist das vollständige Fehlen des 1. und 2. Halswirbels sowie der Knochen des Autopodiums.

Schlachtspuren

An verschiedenen Unterkiefern lassen sich an der buccalen Seite des Corpus feine Schnittspuren feststellen (Abb. 1). Sie befinden sich meist dort, wo die Haut sehr eng am Knochen anliegt. Selbst mit heutigen feinsten Instrumenten können solche Schnittspuren nicht vermieden werden (L. Vinciguerra, pers. Mitt.). Im Ramus von vier Unterkieferhälften befinden sich offensichtlich absichtlich angebrachte kleine Löcher von 3–5 mm Durchmesser (Abb. 2).

Artbestimmung

Am lebenden oder frischtoten Tier gibt es verschiedene Möglichkeiten, *M. martes* und *M. foina* zu unterscheiden: Form und Farbe des Kehlflecks, Behaarung der Pfoten, Kopfform, Dichte und Farbe des Felles, Nasenspiegel (Buchalczyk 1981; Stubbe 1988).

Liegen nur Knochen vor, dienen folgende metrische und nichtmetrische Merkmale an

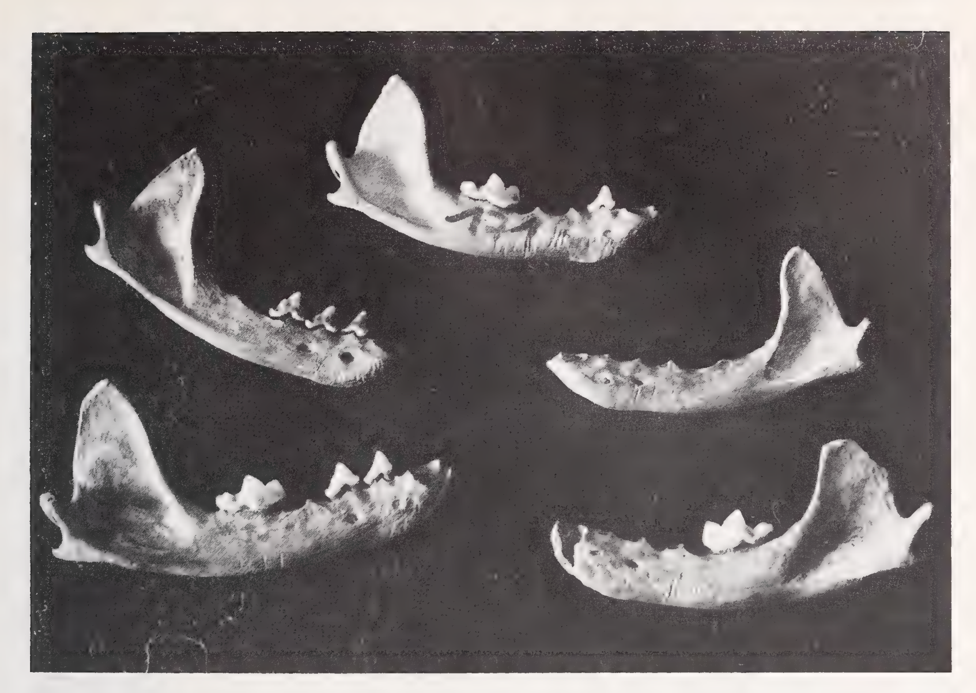


Abb. 1. Mandibulae von *Martes martes* mit deutlichen Schnittspuren (Herkunft: neolithische Siedlung Twann)



Abb. 2. Mandibulae von *Martes martes* mit Löchern im Ramus mandibulae (Herkunft: neolithische Siedlung Twann)

Schädel und Unterkiefer der Artbestimmung: Form und Proportionen des Schädels, Form der Nasenöffnung, Lage und Distanz der Foramina mentalia, Unterschiede am Gebiß, Ausformung des knöchernen, äußeren Gehörganges, Ausbildung der Postorbitalregion (Buchalczyk 1981; Gaffrey 1953; Rode und Didier 1944; Steiner und Steiner 1986; Stubbe 1988).

Da die Anwendung subjektiver Kriterien an einem zahlenmäßig beschränkten Material problematisch ist, wurde versucht, nur mit Hilfe metrischer Merkmale zu arbeiten.

Gerasimov (1985) unterscheidet verschiedene metrische Systeme, um *M. martes* und *M. foina* zu trennen. Eines davon berücksichtigt die Distanz der normalerweise in zweifacher Ausführung vorhandenen Foramina mentalia (manchmal ist nur eines ausgebildet, in seltenen Fällen mehr als zwei). Dieses Maß wird zur Kieferlänge (Processus condyloideus bis Vorderrand der Alveole des I_1) in Beziehung gesetzt (Stampfli 1976). Abbildung 3 zeigt die Einzelwerte sowie die 90%-Ellipsen der erwähnten Maße von *M. martes* und *M. foina*. Ein ♀ aus der Sammlung Bern wurde in dieser Darstellung nicht erfaßt, da eine Fehlbestimmung nicht ganz ausgeschlossen werden kann. Aufgrund der identischen Lage der Meßwerte der rezenten *Martes martes* und der Marder aus Twann darf mit großer Wahrscheinlichkeit angenommen werden, daß letztere vom Baummarder stammen.

Nach Gaffrey (1953) sollte das hintere Foramen mentale bei *M. martes* unterhalb der hinteren Wurzel von P_3 liegen. Bei 60 % der Twanner-Unterkiefer liegt es an dieser Stelle. In neun Fällen (von 25) liegt es zwischen der hinteren und der vorderen Wurzel des P_3 und einmal sogar unterhalb dessen vorderer Wurzel.

Die Vermutung, daß sich die beiden Marderarten aufgrund des Anteils von Länge Trigonid an der Gesamtlänge des M_1 unterscheiden könnten (wegen unterschiedlich stark carnivorer Ernährungsweise, van Valkenburgh 1989; Wolsan et al. 1985), bestätigte sich am rezenten Vergleichsmaterial nicht. Dieses Kriterium wurde daher für eine Artbestimmung im vorliegenden Material nicht herangezogen. Offenbar unterscheiden sich die beiden Arten in ihren Ernährungsgewohnheiten zu geringfügig, als daß sich das am Gebiß manifestieren würde. Marchesi et al. (1989) finden zwischen *M. martes* und *M. foina* der gleichen Region kleinere Unterschiede im Nahrungsspektrum als zwischen mehreren

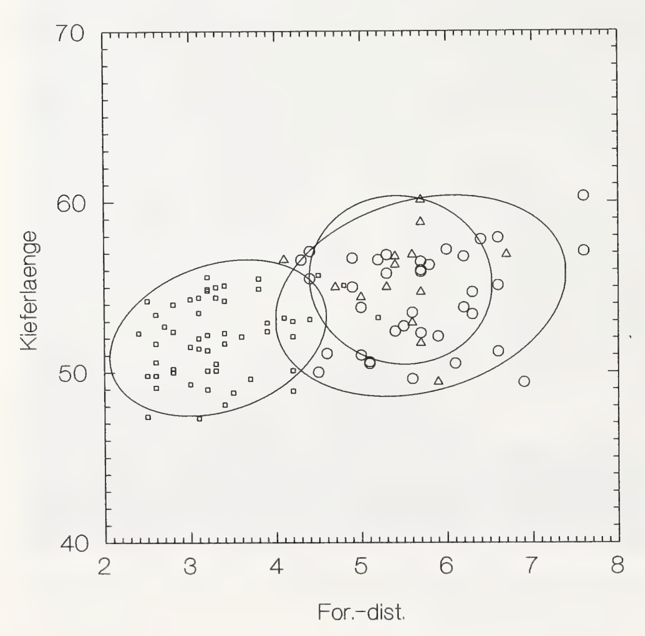


Abb. 3. Einzelwerte und 90%-Ellipse von *Martes foina* rezent (□), *Martes martes* rezent (○) und *Martes* spec. Twann (△). Abszisse: Distanz der Foramina mentalia voneinander; Ordinate: Mandibula-Länge vom Processus condyloideus bis zum Infradentale

M. foina-Populationen aus verschiedenen Gebieten. Die Unterschiede zwischen den beiden Arten sind in den wichtigsten Beutegruppen mehr quantitativer als qualitativer Art. Clutton-Brock (1990) ordnet die Marderunterkiefer der neolithischen Station Yvonand IV in Anlehnung an die von Anderson (1970) publizierten Daten *M. martes* zu. Es gilt jedoch zu beachten, daß Andersons Trigonidwerte von *M. foina* innerhalb der Variationsbreite derjenigen von *M. martes* liegen.

Geschlechtsbestimmung

Unter der Annahme, daß das gesamte Marderknochen-Material vom Baummarder stammt, kann versucht werden, die vorhandenen Meßwerte den ♂♂ oder den ♀♀ zuzuordnen.

Die Variationsbreiten der Unterkiefermaße von rezenten Baummarder-Weibchen und -Männchen zeigen einen großen Überschneidungsbereich. Es können somit nicht ohne weiteres zwei Gruppen unterschieden werden.

Abbildung 4 zeigt die Werte der Länge des Processus condyloideus korreliert mit der Backzahnreihe rezenter Baummarder. Innerhalb der untersuchten Meßreihe kann jedes

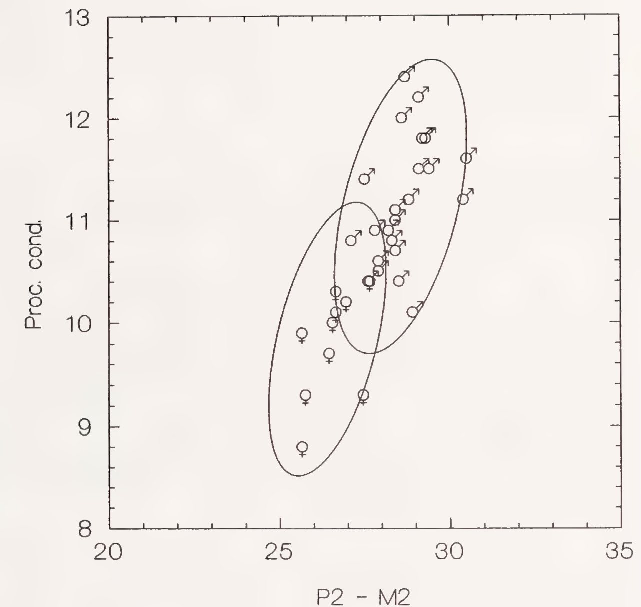


Abb. 4. Einzelwerte und 90%-Ellipse von rezenten *Martes martes* ♂ und ♀. Abszisse: Backzahnreihe (P_2–M_2); Ordinate: Breite des Processus condyloideus

Individuum mit einer unterschiedlich hohen Wahrscheinlichkeit dem einen oder anderen Geschlecht zugewiesen werden. Es zeigte sich, daß die beiden erwähnten Maße die an sie gestellten Erwartungen erfüllen. In Abbildung 5 sind auf die gleiche Art die Unterkiefermaße aus Twann dargestellt (ein Unterkiefer wurde für diese Abbildung nicht mitberücksichtigt, da seine Maße extrem außerhalb aller anderen liegen).

Um den Geschlechtsdimorphismus an den Langknochen zu prüfen, muß auf das dänische Vergleichsmaterial zurückgegriffen werden. Die 4–5 ♂♂ und 2–3 ♀♀ unterscheiden sich in der Größe recht deutlich voneinander. Bei keiner der gemessenen Strecken konnte ein Überschneidungsbereich der beiden Geschlechter festgestellt werden. Im Gegensatz dazu lassen sich die Marder aus Twann nicht eindeutig in zwei Gruppen aufteilen (statistische Werte der Maße der neolithischen Tiere s. Tab. 2). Untersuchungen an polnischen (Reig und Ruprecht 1989) und an schwedischen Mardern (Reinwaldt und

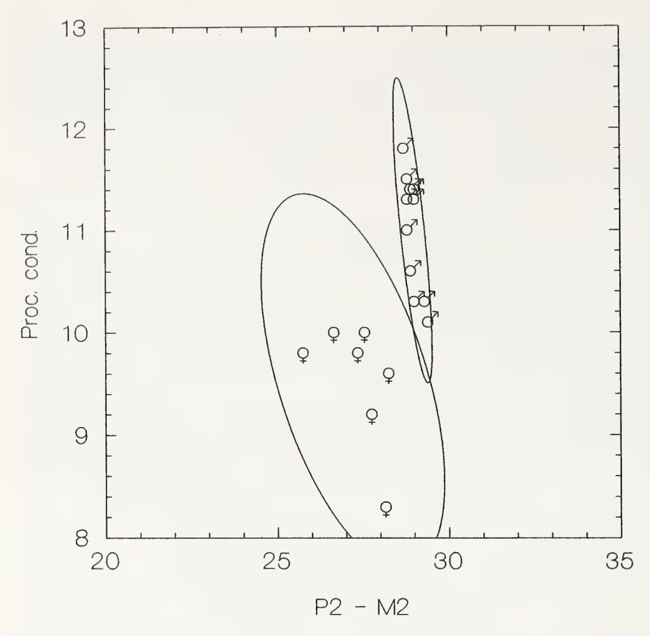


Abb. 5. Einzelwerte und 90%-Ellipse von *Martes martes* ♂ und ♀ aus Twann. Legende s. Abb. 4

Erkinaro 1959) zeigen ebenfalls einen ausgeprägten Sexualdimorphismus, der sich am Schädel deutlicher manifestiert als an den Langknochen.

Größenvergleich

Sämtliche Schädel- und Unterkiefermaße der neolithischen Marder aus Twann liegen innerhalb der Variationsbreite derjenigen der rezenten, die Mittelwerte der erstgenannten sind jedoch höher. Der Vergleich der Langknochenmaße ergibt ein etwas anderes Bild: Die neolithischen Marder aus Twann waren, verglichen mit den neuzeitlichen Tieren aus Dänemark, etwas kleiner bis gleich groß. Werden die Baummarder aus Twann mit solchen aus anderen neolithischen Stationen verglichen (Burgäschisee-Süd, Auvernier, Yvonand), ergibt sich eine recht einheitliche Größe.

Diskussion

Skelettverteilung

Die grundlegenden Strukturen von Siedlungsschichten und deren Inhalt sollen hier nicht erörtert werden. Es stellt sich im vorliegenden Zusammenhang jedoch die Frage, wieso Unterkiefer im Vergleich zu anderen Knochen überrepräsentiert sind. Die relativ feinen, aber deutlichen Schnittspuren an den Mandibeln sowie das Loch im Processus articularis lassen eine zweckdienliche Nutzung dieser Unterkiefer vermuten. Die Beschreibung eines durchbohrten, polierten Marder-Unterkiefers aus der Horgener- Schicht von Eschner-Lutzengüetle (Hartmann-Frick 1960) weist in die gleiche Richtung.

Das Fehlen der entsprechenden Schädel, Wirbel sowie der Knochen des Autopodiums mag ein Hinweis darauf sein, daß die gefundenen Knochenreste von Mahlzeiten (verkohlte Knochen) stammen bzw. Zeugen sonstiger Nutzung (Mandibeln) sind. Die Knochen des Autopodiums blieben vermutlich beim Häuten des Tieres im Fell bzw. wurden als Abfall weggeworfen.

Tabelle 2. **Baummarder *(M. martes)* aus Twann: Statistische Werte**

Schädel

M1: Mediane Gaumenlänge, M2: Prämolarenreihe, M3: Größte Länge des Reißzahnes, M4: Größte Breite des Reißzahnes, M5: Schädelenge, M6: Stirnbreite, M7: Breite über die Eckzahnalveolen, M8: Breite zwischen den Orbitae. n: Anzahl Meßwerte, M: Durchschnitt, SD: Standardabweichung, Min: kleinster Wert, Max: größter Wert

	M1	M2	M3	M4	M5	M6	M7	M8
n	1	3	3	3	1	2	1	2
M	42,1	19,80	8,47	5,57	19,6	21,90	16,3	19,45
SD		0,17	0,76	0,70				
Min		19,7	7,8	4,9				
Max		20,0	9,3	6,3				

Unterkiefer

M1–M5, M8, M9 stimmen mit den entsprechenden Definitionen in von den Driesch (1976) überein; M6: Größte Länge des Reißzahnes, M7: Größte Breite des Reißzahnes, M10: Distanz zwischen den beiden Foramina mentalia

	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10
n	15	15	18	18	23	19	18	17	28	21
M	55,31	53,23	48,67	46,49	29,96	10,25	4,45	24,45	9,86	5,47
SD	2,82	2,59	3,07	2,72	1,77	0,52	0,34	1,95	0,88	0,56
Min	49,4	48,0	42,6	40,7	25,7	9,0	3,9	21,2	8,0	4,0
Max	59,8	57,4	54,1	50,8	32,6	11,3	5,4	27,3	11,7	6,7

	Scapula			Humerus		
	GLP	KLC	GL	GL	Tp	Bd
n	5	6	3	4	8	15
M	11,50	9,45	43,47	67,18	12,70	14,37
SD	0,50	0,54	0,81	4,36	0,90	0,78
Min	10,6	8,6	42,9	63,3	11,9	12,7
Max	11,8	10,2	44,4	71,1	14,3	15,4

	Ulna			Radius			Pelvis	
	GL	KTO	BPc	GL	Bp	Bd	LAR	LFo
n	3	6	6	5	8	5	10	3
M	63,67	7,20	6,57	54,78	6,69	8,40	8,26	16,33
SD	3,07	0,36	0,37	3,97	0,78	0,78	0,61	0,70
Min	61,2	6,8	6,2	49,4	5,5	7,4	7,5	15,6
Max	67,1	7,6	7,2	60,3	7,8	9,4	9,3	17,0

	Femur				Tibia		
	GL	Bp	TC	Bd	GL	Bp	Bd
n	4	9	10	9	5	8	10
M	76,68	14,44	7,00	13,77	83,78	13,66	9,87
SD	4,77	1,02	0,36	1,36	4,64	1,22	0,65
Min	72,4	13,0	6,6	12,1	78,8	11,4	8,5
Max	81,0	15,7	7,6	15,6	89,0	14,8	10,5

Das Fehlen des Steinmarders, *Martes foina*

Im untersuchten Knochenmaterial von Twann konnte nur *M. martes,* nicht aber *M. foina* nachgewiesen werden. Entsprechendes gilt für andere neolithische Siedlungen (Yvonand IV: Clutton-Brock 1990; Feldmeilen-Vorderfeld: Eibl 1974; Egolzwil 2: Hescheler und Rüeger 1939; Burgäschisee-Süd: Jéquier 1963; Auvernier: Stampfli 1976; Schenkon-Trichtermoos: Stampfli 1974). Ausnahmsweise finden sich in den Listen neolithischer Grabungen auch Knochen von *M. foina,* allerdings ohne Hinweis auf die Artbestimmung (Eschner-Lutzengüetle: Hartmann-Frick 1960; Yverdon-Garage Martin: Chaix 1976).

Diese Tatsache wirft Fragen über Verbreitung und Nutzung dieser beiden Tierarten in der Vergangenheit auf.

EHRET (1964) und PIEHLER (1976) stellen in römerzeitlichen städtischen Siedlungen noch das Fehlen von *M. foina* fest. TEICHERT (1989) weist den Steinmarder im Gebiet der ehemaligen DDR erstmals in der Slawenzeit nach. Nach ANDERSON (1970) ist der Steinmarder in Europa erst „in late postglacial times" fester Bestandteil der Fauna. Sie vermutet sein Eindringen vom mittleren Osten her, wo er in würm- und nacheiszeitlichen Ablagerungen nachgewiesen werden konnte. Nach seiner nordwestwärts gerichteten Ausbreitung besetzte er ungenutzte Nischen und entwickelte sich zum Kulturfolger.

Unter der Annahme eines gleichzeitigen Vorkommens der beiden Marderarten stellt sich jedoch die Frage nach einer möglichen Präferenz durch die ur- und frühgeschichtlichen Menschen. Die Felle der Tiere waren sicher ein geschätzter Rohstoff (BUTZECK 1989). Der Baummarder als besser kälteangepaßte Art weist ein deutlich dichteres Fell auf als der Steinmarder (MÜRI 1982; STUBBE 1988). Noch heute werden Baummarderfelle ihrer besseren Qualität wegen bis doppelt so hoch bezahlt wie diejenigen vom Steinmarder (GAUTSCHI 1984).

Da die Marder ihrer nächtlichen Lebensweise wegen wahrscheinlich mit Fallen und Schlingen erlegt wurden, scheint es fragwürdig, ob die neolithischen Menschen oben erwähnte bessere Fellqualität auszunutzen wußten.

Geschlechterverteilung

Verschiedene Gründe können für das Überwiegen von Knochen männlicher Marder im Material (sowohl Langknochen wie Unterkiefer) verantwortlich sein. Männchen haben von Natur aus größere Aktionsräume als Weibchen (SCHRÖPFER et al. 1989), laufen also erhöht Gefahr, gefangen zu werden. Als Vergleich dazu mögen Zahlen aus dem Naturhistorischen Museum Bern dienen: Bei den meisten Carnivoren – so auch bei den Mardern – sind bedeutend mehr Schädel männlicher Tiere in den Sammlungen zu finden, da diese häufiger verunfallen als die weiblichen Artgenossen. Gefangene ♀♀ bzw. ihr Analdrüsensekret können als Köder beim Fang weiterer Tiere dienen, was jedoch wiederum ein Überwiegen der ♂♂ ergibt (diese Fangmethode wird heute noch in Afrika, z.B. für die Fuchsmanguste, *Cynictis penicillata,* durch die einheimische Bevölkerung angewendet; L. VINCIGUERRA, pers. Mitt.).

Größenvergleich

DEGERBØL (1933) stellt für dänische Verhältnisse fest, daß die postglazialen Baummarder (n = 39) größer und kräftiger gebaut waren als die rezenten Tiere, was sich vor allem in der Größe des unteren Reißzahnes manifestiere. Für die Baummarder von Egolzwil (n = 5, HESCHELER und RÜEGER 1939) gilt das Gegenteil: die heutigen Tiere sind ihnen an Größe überlegen. Eine dritte Variante beschreibt JÉQUIER (1963) für die Baummarder in Burgäschisee-Süd (n = 4): Sie sind ungefähr gleich groß wie die rezenten Vergleichstiere.

ANDERSON (1970) erwähnt, daß, obwohl die postglazialen Tiere größer sind als die rezenten, ein Überschneidungsbereich vorhanden sei. Diese Feststellung könnte die vorliegende Untersuchung, die in einzelnen Maßen eine minimale Größenzu-, in anderen eine ebenso geringe Größenabnahme ergibt, bestätigen, dürfte möglicherweise auch die unterschiedlichen Resultate von DEGERBØL (1933), HESCHELER und RÜEGER (1939) sowie JÉQUIER (1963) erklären. Bei der Interpretation so kleiner Größenunterschiede darf nie vergessen werden, daß evtl. auch klimatische und ökologische Faktoren mitspielen, bzw. daß bei einem subfossilen Material stets auch die Unsicherheit der Geschlechtsbestimmung mitspielt (was bei so geringem Material um so stärker ins Gewicht fällt).

Danksagungen

Für die Überlassung des Materials und für die großzügige finanzielle Unterstützung der vorliegenden Arbeit möchte ich dem archäologischen Dienst des Kantons Bern herzlich danken. Die Bereitstellung modernen Vergleichsmaterials verdanke ich den Naturhistorischen Museen in Bern, Basel und Genf. Mein Dank geht ebenfalls an Marc Nussbaumer, der mir bei der statistischen Auswertung behilflich war.

Zusammenfassung

149 Knochen von *Martes* sp. aus der neolithischen Ufersiedlung von Twann (Bieler See, Schweiz) waren Gegenstand einer osteometrischen Untersuchung. Schnitt- und Brandspuren lassen vermuten, daß die Marder ihres Felles, wahrscheinlich aber auch ihres Fleisches wegen gejagt worden waren. Mit Hilfe rezenter Vergleichsskelette konnte eindeutig festgestellt werden, daß es sich bei den vorliegenden Knochen um solche des Baummarders, *Martes martes*, handelt. Mittels Clusteranalyse gelang es, die vorhandenen Unterkiefer männlichen bzw. weiblichen Tieren zuzuordnen. Bei den Langknochen scheint der Überschneidungsbereich der Maße zu groß zu sein, als daß alle vorliegenden Knochen eindeutig dem einen oder anderen Geschlecht zugewiesen werden könnten.

Der Vergleich mit Baummarderknochen anderer neolithischer Stationen zeigt eine einheitliche Größe der Tiere. Anhand der Schädel- und Unterkiefermaße kann eine leichte Größenabnahme vom Neolithikum bis zur heutigen Zeit festgestellt werden.

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The Alpine marmot (*Marmota marmota* L.) in the Spanish Pyrenees

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Abstract

Studied the distribution and colonization process of Alpine marmot (*Marmota marmota* L.) in the Southern Pyrenees. Marmots became extinct at the end of the Pleistocene in the Pyrenees, and have been introduced since 1948 on the northern slope of the mountain range (France). More than 350 localizations have been recorded. Results show factors that have affected its expansion, such as: orographic barriers, mountain passes, habitat selection and human disturbance. Location is given in 2 × 2 km of the UTM squares, which indicates the existence of at least one colony. Colonies range from 1450 to 2900 m, more frequently between 1800 and 2400 m height. A positive correlation exists between the years of existence in each massif and the altitudinal range ($r = 0.89$, $p < 0.01$), and between the maximal height of the massif and the maximal height of the colonies ($r = 0.80$, $p < 0.01$).

Introduction

The Alpine marmot inhabited the Pyrenees during the Pleistocene (Altuna 1965; Besson 1971; Villalta 1972). At the end of this period it only survived in the Alps (*Marmota marmota marmota*) and in the Carpatian mountains (*Marmota marmota latirostris*). After 1948 (Couturier 1955) several deliberate introductions were undertaken either by official organizations such as the Parc National des Pyrénées Occidentales (P. N. P. O.) or by hunters, which have continued to date (Olivier 1979; Dubreuil 1989; Novoa, pers. comm.)

There were various motives for these activities. Couturier (1955) attempted to reduce the impact of the golden eagle (*Aquila chrysaetos*) preying on the chamois (*Rupicapra pyrenaica pyrenaica*), while Chimits (1971) intended the marmot to be an alternative feeding source for the brown bear (*Ursus arctos*) and thus to lessen the latters attacks on livestock (Buffiere 1988; Chaumeil 1988). The marmot became established in Spain since at least 1968 and is now widely distributed over the entire southern slope of the Pyrenees (Garcia-Gonzalez et al. 1985).

The aim of this paper is to describe the distribution of this species and to outline its colonising process. From this information it is expected that factors having conditioned the spread of this species can be elucidated.

Material and methods

The data for the colonies established on the Spanish slope have been obtained by means of inquiries, revision of bibliographical sources and mainly systematic investigation of the landscape. The inquiries were carried out on mountain people, livestock managers and above all the rangers of the various organizations responsible for wildlife management: Diputación General de Aragón (D. G. A.), Generalitat de Catalunya, Diputación Foral de Navarra (D. F. N.).

The surveys have revealed a great deal about the development of the colonizing process (Canut et al. 1989; Herrero et al. 1987). The bibliographical revision of Olivier's (1979) thesis has provided

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information on the French deliberate introductions and on the first marmot localities in the Iberian Peninsula. Systematic exploration of the land was undertaken to test the validity of these inquiries. More than two hundred colonies have been visited since 1984, especially systematically in the summers of 1988 and 1989. In 1990 some new data were added. We have thus been able to gather information about the ecological features of the habitat.

On most of these expeditions we were accompanied by the afore-mentioned rangers. Location of colonies was made easier by the use of a dog. This method has been used with various ground squirrel species (Zwickel 1980) including *Marmota vancouverensis.* (Munro et al. 1985).

Results and discussion

The colonizing process

The analysis of historical and present-day Alpine marmot distribution on the southern slope of the Pyrenees enables us to deduce the factors, both physical and human, which have influenced its expansion (Herrero et al. 1987). The Spanish locations where colonisation has taken place most closely correspond to the French areas where the introduction has been nearest to the border and/or most abundant. In many cases the marmot has only taken two or three years to establish on the Spanish territory (Gonzalez-Prat et al. 1989).

Dispersion is delayed but not prevented by high massifs or steep slopes, as they act as orographic barriers. Mountain passes provide passage ways leading to colonization of other slopes, especially those below 2400 m altitude. Habitat selection is also an important factor in the colonising process and the marmot's preference for southern slopes is extremely influential. The features of French northern slope being less suitable, have favoured the expansion throughout the Spanish Pyrenees.

Human presence and the construction of infrastructures has made marmot colonization difficult, according to what has been discovered by the explorations. Tranquillity having been restored, however, some previously disturbed areas are quickly reoccupied.

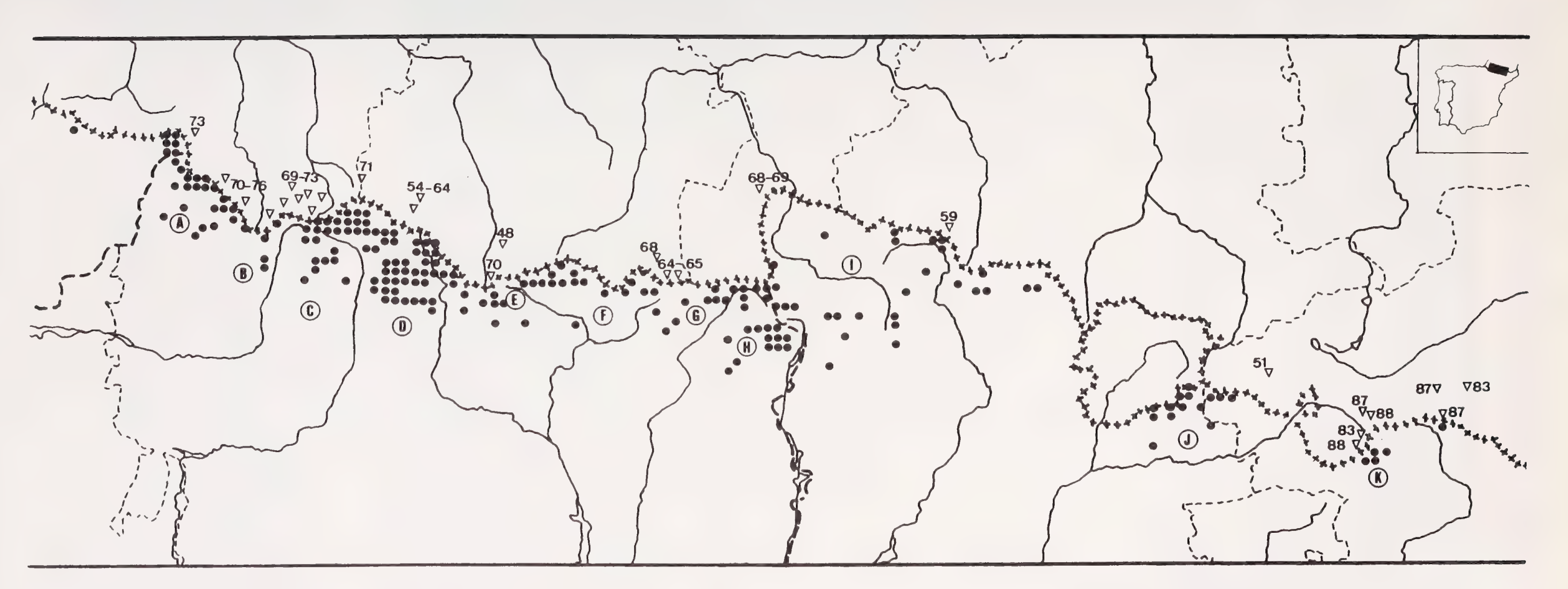
Current distribution

The Figure shows the current distribution of the marmot over the southern Pyrenees, taken from points superimposed on a UTM grid of 2 km side. Therefore marmots can be found in at least 190 squares of 4 km^2 (11 % of the area between 1600 and 2400 m). The height ranges between 1800 and 2400 m altitude, although there are extreme localities at 1450 and 2900 m (Herrero and Garcia-Serrano 1989).

The most westerly point was of a marmot in spring dispersion. The area between this one and the nearest localities has not been specifically explored.

The Table shows the first year of marmot presence, the number of colonies and the altitudinal range occupied by this animal throughout the southern slope of the Pyrenees with differentiated geographical sectors. A positive correlation between maximum altitude of the massif and maximum altitude of marmot colonies can be seen ($r = 0.8067$, $p < 0.01$). Between the maximum height of the massif and the minimum altitude of colonies, however, there is no significant relationship ($r = 0.375$, $p < 0.1$). There is, therefore, a natural upper limit conditioned by there being an occupiable habitat that is higher in relation to the height of the massif. The lower limit (tolerance interval of an average of 1813 m $\pm$ 227 m) does not depend on the height of the massif. One conditioning factor could be human activity (livestock, forestry), which has lowered the natural limit above tree-line, and has widened the supraforestal pastureland (subalpine alpinized level) and therefore the ideal habitat for the marmot. This upper forest limit has been established heterogeneously depending on the specific exploitation of the valley.

The age of the first marmot locality for each massif is positively correlated to the



Distribution of Alpine marmot in southern Pyrenees (Spain). Location is given in 2 × 2 km UTM scale. Triangles and numbers indicate the site and year of the first introduction in France. Letters indicate the sector mentioned in the table. The border is drawn with crosses

First observed date, number of colonies and altitudes of marmot colony recorded in southern Pyrenees

Letters in brackets correspond with the sectors repesented in the figure

Massifs and max. height	1st date presence	Max. height	Min. height	Number of colonies
Massif of Anie, Alanos, Peña Forca 2504 m (A)	> 1980	1900	1500	29
Massif of Bisaurin and Sa of Aisa 2676 m (B)	> 1970	2280	1400	39
Aragón-Gállego watershed 2886 m (C)	> 1970	2200	1700	12
Gállego-Ara watershed 3144 m (D)	1968	2700	1500	150
Monte Perdido Massif 3355 m (E)	1978	2500	1900	10
Cinca and Cinqueta valleys 3174 m (F)	1968	2650	1450	16
Posets 3371 m (G)	1978	2400	2000	18
Maladeta Massif 3404 m (H)	1967	2900	1850	40
Pallars 3015 m (I)	1975	2375	2000	18
Cerdanya 3143 m (J)	1982	2700	2450	19
Nuria 2910 m (K)	1984	2250	2200	5

altitudinal range (maximum versus minimum height) occupied at present ($r = 0.8941$, $p < 0.001$), although this is not the case with the number of colonies observed in these ranges ($r = 0.43$, $p > 0.1$), or the altitudinal range with the number of colonies ($r = 0.59$, $p > 0.05$).

This may indicate that the marmot has tended to increase its expansion, colonising the whole potentially occupiable altitudinal range. Some massifs have been shown to be particularly advantageous, especially the Gállego-Ara watershed, sector D, whereas others are less suitable for habitation. This heterogeneous colonisation is most likely the reason for a lack of correlation between the altitudinal range and the number of colonies. The colonisation process has not yet finished and there are various massifs which are likely to become occupied soon, such as Cotiella and Turbón.

Acknowledgements

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Alistair Danson and Joachim Griesinger did the English and German translations, respectively.

Zusammenfassung

Die Murmeltiere (Marmota marmota L.) in den spanischen Pyrenäen

Untersucht wurde die fortschreitende Besiedlung und Ausbreitung des Murmeltieres in den südlichen Pyrenäen. Murmeltiere starben in den Pyrenäen am Ende des Pleistozäns aus und wurden seit 1948 auf der nördlichen französischen Seite wieder eingeführt. Über 350 Beobachtungsdaten gingen in die Untersuchung ein. Die Ergebnisse zeigen, daß Faktoren wie orografische Barrieren, Gebirgspässe, Wahl des Lebensraumes und Störungen durch den Menschen die Ausbreitung des Murmeltieres beeinflußt haben. Die Daten sind in Quadraten von 2×2 km (UTM-Gitter) angegeben, worin sich mindestens eine Kolonie befindet. Die Kolonien reichen von 1450 m bis 2900 m Höhe, sind jedoch häufiger zwischen 1800 m und 2400 m Höhe.

Es besteht ein positiver Zusammenhang zwischen Zeitdauer der Anwesenheit der Tiere und ihrer Besiedelung der Höhenstufen in jedem Bergmassiv ($r = 0.89$, $p < 0.01$) sowie zwischen Maximalhöhe des Massives und Höhe über NN der angesiedelten Kolonien ($r = 0.80$, $p < 0.01$).

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New data on the systematics and karyology of *Podoxymys roraimae* (Rodentia, Cricetidae)

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Abstract

Sixty years after its first description by H. E. Anthony, the second record of the monotypic akodontine cricetid *Podoxymys roraimae* was obtained at the type locality, the summit of the Roraima tepui, Venezuela. It was a juvenile female with little tooth wear. The new specimen permitted an updated description of the species, and a more precisely characterization of its molar teeth, which have clearly defined bunodont cusps and well developed mesolophids. *Podoxymys* is more closely related to *Microxus bogotensis* than to species of *Oxymycterus*. The concept of an oxymycterine group is discussed and rejected on the basis of recent electrophoretic results. Thus, the similarities between *Podoxymys* and *Oxymycterus* are better considered as a result of convergence. Analysis of standard metaphase chromosomes of the new individual resulted in a particularly low-numbered karyotype of 2n = 16. The occurrence of low-numbered karyotypes in different groups of eutherian mammals indicates that genome condensation in a few chromosome pairs occurred independently in different phylads. In the Akodontini, two such phylads occur, one involving Brasilian forms, and another comprising a group of species of *Akodon* from the northern Andes. *Podoxymys* is more likely to belong to the latter, both by biogeographical reasons, and because of its close resemblance with the Venezuelan *Microxus bogotensis*.

Introduction

The tepuis are tableland high elevations that rise abruptly interspersed within the forests and savannas of northeastern South America. They lodge a unique flora and fauna which has long attracted the attention of naturalists by the high frequency of generic and specific andemisms (Mayr and Phelps 1967; Steyermark, 1986; Ochoa and Gorzula 1992). Among mammals, one outstanding example of such an endemism is *Podoxymys roraimae*, a species of a monotypic genus of akodontine cricetid mice only known from the summit of the Roraima tepui, which rises up to above 2700 m in the southeastern corner of Bolivar State (Venezuela). This species was described by Anthony (1929) on the basis of 5 specimens. Up to now no additional specimens have been found. Apart from the original brief description by Anthony, those specimens were the basis of further partial descriptions of its anatomy by Gyldenstolpe (1932), Carleton (1973), and Hinojosa et al. (1987). Recently, one individual was obtained during a brief expedition organized by the La Salle Natural History Museum of Caracas (MHNLS) in June, 1989. The new specimen allowed to advance in the knowledge of the anatomy and systematics of this rare mouse, and the acceptably successful preparation of chromosomes in the field permitted to report for the first time its standard karyotype.

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Material and methods

The single specimen of *P. roraimae* reported herein was a young female obtained during the night or early morning of June 1, 1989. It was captured on a line of 100 Sherman live-traps laid at 2628 m a. s. l. at the summit of the Roraima mountain. The trap line was set for six nights on a surface covered by a carpet of the moss *Sphagnum* sp. in which various small cavities were scattered. The overall yield was one *P. roraimae* and four *Rhipidomys macconnelli.* Skins and skulls of all specimens were deposited in the MHNLS, Caracas, were those of *P. roraimae* bear cataloque number MHNLS-8860. This specimen was compared with notes and drawings of original specimens of *P. roraimae* taken previously by one of the authors (OAR) at the American Museum of Natural History. Direct comparisons have also been made with specimens of *Akodon, Oxymycterus, Microxus,* and other South American cricetids from different collections. Fur and hair colors follow Smithe (1975). Standard body and cranial measurements were taken with a Vernier calliper (app. 0.1 mm) and the eye piece of a stereomicroscope (app. 0.01 mm). All measurements are given in mm. Nomenclature of enamel components of the molar teeth, follows Reig (1977). Metaphase chromosomes were obtained in the field by the bone marrow method (Reig et al. 1971), and stained with Giemsa. Ten karyotypes were constructed from enlarged photographic prints, and the lengths of chromosomes and chromosome arms were measured, averaged and expressed as a percentage of the total length of the female haploid set (LHS) (Table) (Reig et al. 1971). Chromosome nomenclature follows Levan et al. (1964), Chromosomes were also assorted into size classes as follows: large-sized equal those > 9 % of LHS; medium-sized, those between 5.5 and 9 %, and small-sized those between 2 and 5.5 %.

Results

Morphology

The data obtained from the new specimen, combined with our data from the original specimens and published information on the stomach (Carleton 1973) allow us to compose the following description of *P. roraimae:*

Size small (head and body about or less than 100 mm) Tail long, as long as or a little longer than head and body. Front claws moderately long (third claw 2.5–3 mm), slender and pointed: claws of the hind feet as in *Akodon*. Fur dense, lax and moderately long, back and sides of head and body, hind feet and tail uniformly dusky-brown (color 19). Hairs long (10 mm on the back), soft and very abundant, blackish (color 82) in most of the length from the base and cinnamon (color 123-A) at the tip. Pelage shortest at the head and the ventral region, where the cinnamon staining is more evident. Eyes very small; ears of small size but clearly visible, although pinnae are partially covered by the dense pelage. Skull (Fig. 1) narrow and slender, with long and narrow muzzle, rather broad interorbital region without trace of supraorbital beading, and a long, deep, moderately inflated and evenly rounded brain case. Upper profile of skull sloping forward from the frontoparietal suture. Nasals shorter than frontals and rather narrow, with posterior ends well behind the fronto-maxillary suture. Anterior borders of nasals and premaxillae moderately projected forward beyond the incisors. Parietals short, less than half the length of frontals. Interparietal reduced. Incisive foramina noticeably long, longer than the cheek tooth row and extending backwards to the hypocone of the first molars. Palate short and broad, extending backward to the level of last molars; cheek-tooth rows divergent to the front. Pterygoid region long; mesopterygoid fossa open in front and parellel-sided. Zygomatic plate reduced, narrow and low and markedly sloping backwards. Zygomatic arches week and thread-like at the middle, scarcely flaring beyond brain-case and gradually diverging backward. Interorbital region broad, smooth and rounded, with supraorbital edges rounded and moderately convergent backward. Bullae slightly inflated and moderate in size. Mandible slender, elongate and proodont, though less so than in *Oxymycterus,* with a short coronoid process and small capsular projection. Upper incisors opisthodont and relatively narrow. Molars rather small and broad, bunodont and brachyodont (Fig. 2). Upper molars with lophs almost completely transverse. In M1 and M2 the main external cusps are subequal, the para- and metaflexus are oriented backward, and enterostyle is

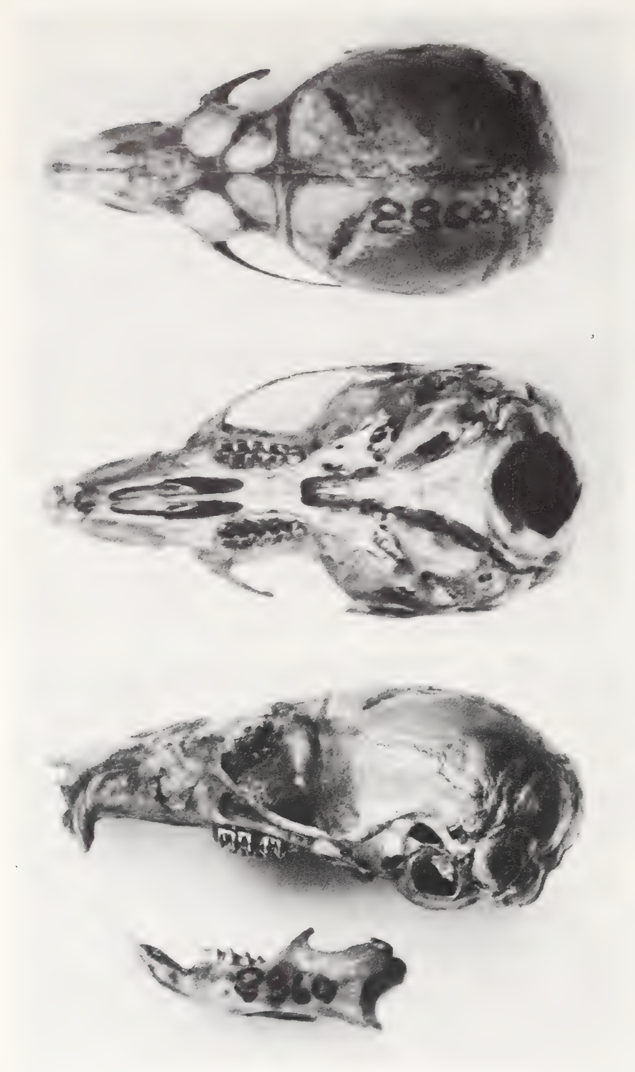


Fig. 1. Skull and lower jaw of a juvenile female of *Podoxymys roraimae* (MHNLS-8860) from the type locality (Roraima mountain, SW of Bolivar State, Venezuela). *Above:* dorsal view of the skull; *middle:* ventral view of the skull; *below:* lateral view of the skull and mandible (enlarged × 2.8)

missing. M1 with somewhat reduced procingulum, with visible anteromedian flexus and anteroflexus in moderately worn teeth, mesoflexus very narrow but present, and mesoloph strongly reduced but not fully fused with paraloph. M2 with mesoloph well developed but low, separated from paraloph by a deep mexoflexus; mesostyle absent. M3 strongly reduced, about ½ the length of M2. Unworn lower molars with opposing cusps somewhat oblique in position, the lingual ones more anterior than the labial ones, tending to a simple prismatic pattern with wear. Procingulum of m1 narrow and simple, without anteromedian flexid. Mesolophid and mesoflexid well developed but low in m1 and m2, and mesostylid absent. Ectolophid and ectostylid may be present in m1, but are absent in m2–m3. Third lower molar moderately reduced, about ¾ the length of m2. Stomach unilocular-hemiglandular, with reduced area of glandular epithelium. Caecum well developed, but very reduced, reaching only 4.4 % of the total intestine length. Large intestine also short.

Measurements of female MHNLS-8860 and of the type specimen, female, AMNH 75586 (in parentheses; omitted when unavailable): Total length 150.0 (196.0); head and body, 72.0 (101.0); tail, 78.0 (95.0); hind foot 21.5 (23); ear, 13.4; greatest length of skull, 24.7 (27.5); length of nasal, 8.5 (11.0); zygomatic breadth, 11.2 (12.3); interorbital breadth, 5.6 (6.0); breadth of rostrum at mid-point, 4.1 (4.2); breadth of brain case, 11.4 (12.3); incisive foramen (length × breadth) 5.8 × 1.7 (7.2 × 2.1); diastema length, 5.9 (6.9); length upper molar row, 4.14 (4.38); length of lower molar row, 4.50 (4.27); M1, 1.79 × 1.24 (2.14 × 1.21); M2, 1.32 × 1.10 (1.40 × 1.21); M3, 0.69 × 0.77 (0.83 × 0.91); m1, 1.79 × 1.18 (1.85 × 1.24); m2, 1.24 × 1.10 (1.31 × 1.19); m3, 1.07 × 0.77 (1.07 × 0.94); total length small intestine, 414.0; total



Fig. 2. Scanning electron microphoto of upper (left), and lower (right) molar teeth of the juvenile female specimen of *Podoxymys roraimae* (MHNLS-8860) from the type locality (Roraima mountain, SW of Bolivar State, Venezuela)

transverse length, blind intestine, 22.0; total measured length, large intestine, 53.0 (actual length must be a little longer, as a small unmeasured cut-off portion must be added); body weight, 10 g.

Cytogenetics

The karyotype of *P. roraimae* is striking by the very low diploid and fundamental (including sex chromosomes) numbers of 2n = 16 and FN = 26 (Fig. 3). The karyotype is formed by five pairs of large biarmed, and three pairs of teleocentric chromosomes. As arranged by size, pair 1 is made by very large metacentrics (Table) separated from the following four elements by a sharp size gap. Pairs 2 and 3 are similar in size, the former being submetacentric and the other metacentric. Pairs 4 and 5 are similarly-sized submetacentrics. A large size gap separates pair 5 from the medium-sized telocentric pair 6, whereas pairs. 7 and 8 are small chromosomes. Therefore, each chromosome pair is very distinctive in size and morphology. As the single studied individual was a female, it is only tentative to identify the X chromosomes. Based on the similarity between the karyotype of *P. roraimae* and that of *Akodon "arviculoides"* (see later) we tentatively identify the chromosomes of pair 7 as the female sex chromosomes.

Statistics of mean lengths of entire chromosomes (T.L.) mean lengths their long (L.L.A.) and their short arms (L.S.A.), and arm ratio (r) and their standard deviations (SD) of *Podoxymys roraimae* from Mount Roraima, Bolivar State, Venezuela

The lengths are expressed as a percentage of the total chromosome length of the female haploid set

Chromosome	T.L.		L.L.A.		L.S.A.		r	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD
1	23.73	.64	12.69	.22	11.14	.38	1.14	.004
2	18.50	.32	12.80	.76	5.51	.14	2.37	.004
3	17.48	.84	9.72	.17	7.91	.50	1.25	.002
4	12.81	.72	7.78	.42	5.03	.35	1.59	.090
5	12.09	.35	7.71	.26	4.38	.09	1.78	.025
6	7.16	.16	7.16	.16	–	–	–	–
7	4.35	.27	4.35	.27	–	–	–	–
8	3.85	.11	2.15	.22	–	–	–	–

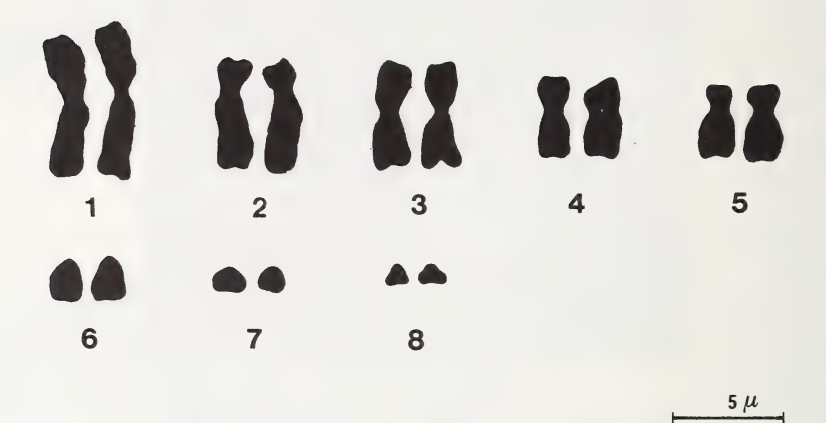


Fig. 3. Giemsa-stained bone-marrow karyotype of *Podoxymys roraimae,* the same specimen of Figs 1 and 2

Discussion

The new specimen matches well enough the holotype and the original description of *P. roraimae* (Anthony 1929) as no casting doubts to its species identification. The differences found in size and morphology reflect the fact that the holotype was an adult with advanced tooth wear, whereas MHNLS-8860 is a juvenile. This allowed us to examine in more detail the molar structure, which resulted peculiar for akodontine standards by the well-developed mesoloph-lophids and the bunodont cusps. However, both in the craneo-dental and digestive system characters, *P. roraïmae* fits well with the diagnosis of the tribe Akodontini (Reig 1987).

Of the eleven recognized extant genera of the Akodontini (Reig 1987), *Podoxymys* was reported to be alike *Oxymycterus* (Anthony 1929) and *Microxus* (Ellerman 1941). Hershkovitz (1966) proposed to distinguish within the akodont rodents an "oxymycterine group", including *Oxymycterus, Podoxymys, Lenoxus, Microxus,* and *Abrothrix* (Hershkovitz considered *Microxus* to be a synonym of *Abrothrix,* but Reig, 1987, found no reasons for such a synonymy). The concept of an oxymycterine group has been recently discussed by Hinojosa et al. (1987), who concluded that it is unclear. Recent electrophoretic data strongly indicate that *Microxus* is more closely related to *Akodon* than to

Oxymycterus, and that the latter is not close to *Lenoxus* (Patton et al. 1989). Besides, *Abrothrix* together with *Chelemys* and *Geoxus* make a subclade of its own clearly differentiated in genetic distance from the remaining Akodontini (Spotorno 1986; Barrantes et al. 1992).

As Ellerman (1941) surmised, *Podoxymys* is probably a close relative of *Microxus.* In fact a closer relationship of *Podoxymys* to *Microxus* than to *Oxymycterus* is expected by distribution, as *Microxus* is represented in the Venezuelan Andes, whereas species of *Oxymycterus* are mostly distributed in the south of South America. We have for comparison specimens referred to *M. bogotensis* from the Andes of Venezuela. Certainly, *M. bogotensis* and *P. roraimae* resemble each other more than any of them resembles species of *Oxymycterus*. They are similar in the relative forward extension of nasals and premaxillae, the degree of reduction of the zygomatic plate, the long frontals, the more reduced interparietal, and the deeper and shorter braincase. However, *M. bogotensis* has a shorter pelage, a much shorter incisive foramina that scarcely reaches the front of first upper molars, parallel cheek teeth rows, and much reduced third molars. Thus, *Podoxymys* may well be a close relative of *Microxus*, but its generic distinction seems to be well warranted.

The karyotype of *P. roraimae* is remarkable by its very low diploid number. Karyotypes with diploid numbers lower than 20 are common among marsupials (Hayman 1990), but they are a rarity (about 1 %) among placentals (Matthey 1973). An extreme case is that of the muntjak deer *Muntjacus muntjak,* with 2n = 6 and 2n = 8 in different subspecies (Wurster and Benirschke 1977; Wurster and Atkins 1972). A karyotype of 2n = 14, with polymorphic variants anf 2n = 15 and 2n = 16 has been described for a Brasilian akodontine erroneously referred to *Akodon arviculoides* (Maia and Langguth 1981; for its nomenclatorial status and references see Liascovich and Reig 1989). A monomorphic 2n = 18 karyotype occurs in the akodontine *Akodon urichi* (Reig et al. 1971), and polymorphic complements of 2n = 16–17 occur in *Nectomys palmipes* (Barros et al. 1992), whereas karyotypes of 2n = 17–18 with odd sex chromosome systems have been reported in the arvicolid voles *Ellobius lutescens* and *Microtus oregoni* (Matthey 1958), and 2n = 18 was also found in the murid *Nannomys* (Mattey 1964). Karyotypes of 2n = 16 are also known in some species of the leaf-nosed bats (Baker 1973).

There are good reasons to maintain that polarity in karyotype number among the Akodontini was from a high-numbered plesiomorphic to a low-numbered apomorphic state (Vitullo et al. 1986; Reig 1987). The same trend was found to be most likely in other tribes of South American cricetids (Gardner and Patton 1976), and in arvicolids (Matthey 1958; Moodi 1987). Thus, the process of condensing the karyotypes to a low number of chromosomes occurred independently in unrelated evolutionary phylads.

Karyotypes of Akodontini cover a wide range of diploid numbers, from 2n = 14 to 2n = 54 (Reig 1987, 1989; Liaskovich and Reig 1989). However, most of the 45 chromosomally known akodontine species have karyotypes within the 2n = 30–44 (42 %) or the 2n = 52–54 classes (Reig 1989). Of *Microxus,* only the karyotype *M. bogotensis* from the Venezuelan páramos is known (Barros and Reig 1979), which is polymorphic with 2n = 35–37. Actually, among the Akodontini, the karyotype of *P. roraimae* is only comparable at the level of chromosome number and gross morphology with the 2n = 14–16 karyotype of *Akodon "arviculoides"*, and that of 2n = 18 of *Akodon urichi.* It is remarkably similar to the 2n = 16 variant of *A. "arviculoides"* from Recife (Maia and Langguth 1981). Both share the same fundamental number, and differ mostly in the first autosomal pair, which is submetacentric in *A. "arviculoides"*, but metacentric in *P. roraimae.* As regards *A. urichi,* the differences are much greater and may involve several rearrangements. Unfortunately, we failed to obtain adequate G-banding karyotypes to test how far the resemblance between *P. roraimae* and *A. "arviculoides"* is due to actual arm sharing.

In fact, a parallel trend towards lower diploid numbers seems to occur within the Akodontini in two independent phylads. Reig (1987) recognized a northern Andean

phylad probably derived from a primitive stock in the soutern puna region showing diploid numbers progressively, although irregularly, decreasing northwards. This phylad includes, among others, species and subspecies of *Akodon* such as *A. aerosus boliolus* (2n = 38), *A. prophilus* (2n = 26), *A. mollis* (2n = 22–23), *A. aerosus* ssp. (2n = 22), *A. torques* (2n = 22) *A. tolimae* (2n = 24), and *A. urichi* (2n = 18) (Reig 1987; Patton et al. 1990). *M. bogotensis* may represent a chromosomally more conservative offshoot of the same branch. As Reig (1987) suggested, *P. roraimae* is likely to be derived from the same stock. We now know that it exemplifies an extreme case of karyotypic reduction consistent with the general trend observed in the northern Andean phylad. But a trend in karyotypic condensation is also evident in an independent phylad which dispersed towards Brasil from a postulated north-central Argentinian dispersal sub-center, as represented by *A. cursor* of Misiones, Paraguay, and south of Brasil (2n = 24), and the karyomorphs of 2n = 14–16 referred to *A. "arviculoides"* from Sao Paulo, Rio de Janeiro and Recife (Liascovich and Reig 1989). The close similarity found between the karyotype of *P. roraimae* and the 2n = 16 karyomorph of *A. "arviculoides"* may be taken as suggesting a closer relation of the tepui akodont to this phylad. However, besides the general disaprowal of hypotheses on phylogenetic relations based on similarities among non-differentially stained karyotypes, there are other reasons to discard this alternative view. There is ample evidence that the tepuian fauna is closely linked to the Andean fauna (Mayr and Phelps 1967). Besides, the areas of distribution of *P. roraimae* and *A. "arviculoides"* are separated by the Amazonian Basin, a region thoroughly deprived of representatives of the Akodontini.

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Zusammenfassung

Neue Unterlagen über die Systematik und Karyologie von Podoxymys roraimae (Rodentia, Cricetidae)

Die akodontine Maus *Podoxymys roraimae*, von H. E. Anthony nach fünf Exemplaren beschrieben und 1929 einer monotypischen Gattung zugeordnet, wurde im Juni 1989 erstmals wieder an der Typuslokalität, dem Gipfel des Roraima tepui in Venezuela, gefangen. Anhand des juvenilen Weibchens und der Originalserie wird eine genauere Beschreibung der Gattung und Art gegeben. *Podoxymys* ist *Microxus bogotensis* ähnlicher als den Arten von *Oxymycterus*. Das Konzept einer oxymycterinen Gruppe innerhalb der Akodontini erscheint unwahrscheinlich und wird auf der Grundlage neuer elektrophoretischer Ergebnisse abgelehnt. Die Ähnlichkeit zwischen *Podoxymys* und *Oxymycterus* ist eher auf Konvergenz zurückzuführen. Die Analyse standardgefärbter Metaphasen des neuen Exemplares ergab eine bemerkenswert niedrige Zahl von 2n = 16 Chromosomen. Ein Vergleich niedriger Chromosomenzahlen bei Säugetieren zeigte, daß die Konzentration des Genoms in wenigen Chromosomenpaaren mehrfach in verschiedenen Stammbaumlinien erfolgte. Innerhalb der Akodontini lassen sich zwei Linien unterscheiden; die eine umfaßt brasilianische Arten, die andere eine Gruppe von *Akodon*-Arten der nördlichen Anden. *Podoxymys* scheint der letzteren nahezustehen, sowohl aus biogeografischen Gründen als auch wegen seiner großen Ähnlichkeit mit dem venezolanischen *Microxus bogotensis*.

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Contribution to the study of the wild House mouse, Genus *Mus* L. (Mammalia, Rodentia, Muridae) in Greece

Study of three populations based on lymphocyte antigen analysis

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Abstract

Typed three Robertsonian wild mice populations from southern Greece, using 16 selected lymphocyte antigens. In all examined mice of the three populations the Thy-1.2 antigen was identified, which is characteristic for the *M. m. domesticus* taxon. On the other hand, the Thy-1.1 allele characteristic for *M. m. musculus* was not found. Moreover, it was indicated that the Ly-1.2 antigen was fixed in these populations while the Ly-1.1 allele was absent. It is already known that although these two alleles cannot be used as markers for the different *Mus* taxa, they can give information about the gene flow between the populations studied.

A polymorphic distribution of the other antigens examined was noted and compared to other European *M. m. domesticus* populations.

It can be concluded from the immunological point of view the studied populations belong to *M. m. domesticus,* and confirms the recent opinions that the Rb populations of *Mus* almost exclusively belong to this taxon.

Introduction

According to many investigators, the entire Greek peninsula is inhabited by two morphologically and biochemically distinct taxa of wild house mice (Bonhomme et al. 1978; Thaler et al. 1981a, b; Bonhomme et al. 1984). One of them belongs to the biochemical group *Mus*-1 and is referred to as *Mus musculus domesticus* Schwarz and Schwarz, 1943 (Darviche and Orsini 1982; Auffray et al. 1990), or as a full species *Mus domesticus* Rutty, 1772. The other taxon belongs to the biochemical group *Mus*-4a, which according to the recent nomenclatorial opinions (Auffray et al. 1990) is *Mus macedonicus* Petrov & Ruzic, 1983.

Many populations of *Mus* in Greece are Robertsonian (Giagia et al. 1987; Tichy and Vucak 1987), i.e., individuals do not have the standard diploid chromosomal number (2n = 40) known for *Mus musculus* but rather karyotypes with 2n = 24, 26, 29, 30 chromosomes. All these variants have occurred by the process of Robertsonian fusion (Robertson and Rees 1916). With respect to the phenomenon of chromosomal repatterning where clearcut instances of speciation processes are very often in progress (Capanna et al. 1977) a clarification of the taxonomic status and inter- and intra-populational relationships of the Rb populations of Greece is needed. Moreover, there is some discussion concerning the presence of Robertsonian populations in subspecies other than *Mus musculus domesticus* (Zima et al. 1990).

Since the classification of different taxa of *Mus* can be undertaken by karyological, genetical and immunological approaches, in this paper we focussed on the immunogenetical approach, based on the study of the major histocompatibility complex (MHC). The MHC is a large chromosome region containing a giant cluster of genes coding for antigens (proteins) which are necessary for functions concerned with the immune response. These

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antigens are polymorphic. At least twenty of them are predominantly expressed on lymphocytes and are therefore referred to as Ly antigens (McKenzie and Potter 1979). Kurihara et al. (1985) using monoclonal antibodies for Thy-1, Ly-1, and Ly-2 antigens demonstrated that in eight *Mus musculus* subspecies examined each possessed characteristic phenotype patterns of these antigens. More recently, Figueroa et al. (1986) confirmed the above observations.

Materials and methods

Mice: Wild mice in this survey belong to three different populations. They were trapped at three localities in southern Greece: 1) Kastritsi (Patras) 25 individuals with 2n = 29, 30, 2) Olympia 10 individuals with 2n = 24 and 3) Theba 10 individuals with 2n = 26, 30. Some of the animals were maintained for a certain period in our laboratory and then transported to Germany (Max-Planck-Institut für Biologie, Abteilung Immungenetik, Tübingen). The remainder of animals were transported immediately after trapping.

Antisera and monoclonal antibodies: The monoclonal antibodies used in this survey were kindly provided by Dr. J. Klein, Max-Planck-Institut für Biologie. These antibodies detect 16 lymphocyte antigens. Most of the antigens are expressed on T cells (Ly 1, Thy 1, L_3T_4, $L_{2,3}$) but some are also expressed on B (Ly 1, Ly 5) cells and other cells such as brain cells, epithelial cells and fibroblasts. All monoclonal antibodies used were obtained from ascites fluid produced by inoculation of inbred cell lines into mice. Other antibodies were obtained from supernatants of a cell line grown in culture.

For details of the antisera used in this assay, see Klein (1972), Zaleska-Rutczynska and Klein (1977), Duncan and Klein (1980), and Figueroa et al. (1986).

Complement-dependent cytotoxic assay: For detection of the antigens in this assay single cell suspensions prepared from thymus and lymph nodes were used. Thymus cells were used for the Thy-1.1, Thy-1.2, Ly-1.1, Ly-1.2, Ly-2.1 and Ly-2.2 antigens and the lymph node cells for the detection of Ly-6.2A, Ly-6.2C, Ly-6.2F, Ly-10, Ly-15.2, Ly-18.2, Ly-17.2, Ly-19.2, Ly-28.2. B_2m antigens (Table 1).

Table 1. **Antigens tested and antibodies used to detect them**

Antigen	Antibody	Reactivity of antibody with	Reference
Thy– 1.1	HO.22.1	T cells	Marshak-Rothstein et al. (1970)
Thy– 1.2	5032–1.3	T cells	Mackenzie and Potter (1979)
Ly – 1.1	7.20.6/3	T cells	Hogarth et al. (1980)
Ly – 1.2	C3PO	T cells	Mark et al. (1982)
Ly – 2.1	49–11–1	T cells	Hogarth et al. (1982)
Ly – 2.2	19–178	T cells	Hammerling (unpubl. data)
Ly – 6.2.A	S8.106	T and B cells	Kimura et al. (1984)
Ly – 6.2.C	SKl42.446	T and B cells	Kimura et al. (1984)
Ly – 6.2.F	TUl92.2.10	T and B cells	Klein et al. (unpubl. data)
Ly –10.1	T18/870	T and some B cells	Kimura et al. (1980)
Ly –15.2	8.6.2	T cells	Potter et al. (1981)
Ly –18.2	S8.261	T and B cells	Kimura et al. (1981a)
Ly –17.(20).2	K9–361	T and B cells	Kimura et al. (1981b)
Ly –19.2	K10.6	B cells	Tada et al. (1981)
Ly –28.2	5075–12.1	T and B cells	Hogarth et al. (1984)
B2m	S19/8	T and B cells	Tada et al. (1980)

Two different complement mixtures were necessary: One with the lymph node cells in rabbit normal serum, guinea pig normal serum, and Hank's balanced salt solution (1 : 1 : 3), and the other one with thymus cells in guinea pig normal serum and Hank's balanced salt solution (1 : 4).

To detect individual Ly antigens in wild mice, the lymph node and thymus lymphocytes of these mice were incubated with monoclonal antibodies in the presence of complement and the percentage of killer cells was estimated. The microcytotoxicity test was carried out in Terasaki microplates (IC. A. Greiner and Sohner, Nürtingen, F.R.G.), as previously described (Zaleska-Rutczynska et al. 1983).

The cytotoxicity was evaluated automatically by the propidium idodide method (Bruning et al. 1982).

Results and discussion

As can be seen from Table 2 each population has a different pattern of lymphocyte antigen frequency. For some of these antigens it is characteristic that either they exist in all examined individuals of the three populations (e.g. Thy-1.2) or they are lacking in all of them (Thy-1.1 antigen). The Thy-1.2 lymphocyte antigen is considered as being characteristic for the individuals belonging to the *M. m. domesticus* taxon (Kurihara et al. 1985). Figueroa et al. (1986) confirmed this observations but with one exception. Two of the eight specimens from Costa Rica, expressed the Thy-1.1 antigen although they belong to the *M. m. domesticus* subspecies. The possible explanation for this finding was either that these two animals are progeny of a mouse in which recurrent mutation caused the Thy-1.2, Thy-1.1 conversion [substitution of a single amino acid at position 89 (Williams and Gagnon 1982)] or these two mice may indicate the existence of Thy-1 polymorphism, perhaps present in some populations of *M. m. domesticus.* The presence of the characteristic Thy-1.2 antigen, in all individuals examined here, verifies their systematic position in the *M. m. domesticus* subspecies, a fact that is in agreement with morphological, biochemical and karyological data (Fraguedakis et al. 1986; Chondropoulos et al. 1992; Giagia et al. 1987; Tichy and Vucak 1987). The study of some of the Ly lymphocyte antigens (Table 2) showed that the Ly-1.2 antigen is fixed in all the examined specimens of the

Table 2. **Frequency of Ly antigens in different populations of wild mice**

Population	No. of animals tested	Antigen frequences							
		Thy–1.1	Thy–1.2	Ly–1.1	Ly–1.2	Ly–2.1	Ly–2.2	Ly–6.2A	Ly–6.2C
Kastritsi	25	0	1.0	0	0.96	0.60	0.20	0.36	0.20
Olympia	10	0	1.0	0	1.00	0.60	0.20	0.20	0.10
Theba	10	0	1.0	0	1.00	0.70	0.40	0.40	0
		Ly–6.2F	Ly–15.2	Ly–18.2	Ly–10.1	Ly–19.2	Ly–17.2	Ly–28.2	B_2m
Kastritsi	25	0.20	0.58	0.36	0.20	0.80	0.52	0.40	0.48
Olympia	10	0.66	0.80	1.00	0.40	0.80	0.80	0.60	0
Theba	10	0.70	0	0.70	0.30	0.70	0.70	0.70	0

population from Olympia and Theba and almost all specimens from Kastritsi, while the Ly-1.1 has not been detected in any specimens of these population samples. These results are in agreement with those of Kurichara et al. (1985) and Figueroa et al. (1986) who also mentioned that for different populations of *M. m. domesticus* there is a characteristic mode of fixation of the antigens Ly-1.1, Ly-1.2, i.e., if the individuals of one *M. m. domesticus* population express the Ly-1.1 antigen, the Ly-1.2 is not expressed and vice versa. From these data, we could conclude that although it is not possible to use these antigens as characteristic markers for the taxonomic possition of the specimens, they could be used as markers for determining the migration rates between local populations (Figueroa et al. 1986). The situation with regard to the Ly-2.1 and Ly-2.2 antigens in this study is as follows. The Ly-2.1 allele is very common in the three populations, while Ly-2.2 only appeared in low frequency. This is one more indication of the homogeneity of the Greek populations. Robinson et al. (1984) mentioned that the B_2m^b allele is characteristic for *M. m. musculus,* since it is present in *M. m. musculus* and absent in the *M. m. domesticus* taxon. Figueroa et al. (1986) reported that half of the wild *M. m. domesticus* populations typed by them, reacted with the B_2m-specific antibody. As can be seen from our results, the B_2m^b allele is absent from the two populations and is present in half of the examined specimens of the third one. These results combined with those of Figueroa et

al. (1986) do not confirm the hypothesis that the B_2m^b allele can be used as a marker for the *M. m. domesticus* taxon.

The typing for the remaining Ly antigen revealed a variability in the frequencies among the three populations studied. Although for the majority of the Ly antigens, our results are in agreement with those of FIGUEROA et al. (1986), some are in contrast. For example, the Ly-28.2 antigen, which the above mentioned authors found to be absent in their collection of wild mice, is present in all our populations. In addition, the Ly-18.2 antigen, which is very rare in the European populations (FIGUEROA et al. 1986), was found frequently in our populations. The reasons for these fluctuations of Ly antigens among the European *M. m. domesticus* populations is at present unknown and remain to be elucidated. According to the present data we can verify that the three examined populations belong to the same taxon *M. m. domesticus,* a conclusion that is in agreement with correlative morphological data. On the other hand, since the three populations are Rb we agree with the opinion of ZIMA et al. (1990) that the Rb populations in the *Mus* species are almost exclusively limited to the range of *M. m. domesticus* taxon.

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Zusammenfassung

Beitrag zu Untersuchungen an der wilden Hausmaus, Gattung Mus L. (Mammalia, Rodentia, Muridae) in Griechenland. Untersuchungen an drei Populationen aufgrund von Analysen mit Lymphozyten-Antigenen

In dieser Arbeit werden drei Robertsonsche Wildmaus-Populationen aus Südgriechenland unter Benutzung von 16 ausgewählten Lymphozyten-Antigenen gekennzeichnet. Bei allen untersuchten Mäusen der drei Populationen wurde das Antigen Thy-1,2 identifiziert, welches typisch für das Taxon *M. m. domesticus* ist. Ferner zeigte sich, daß das Ly-1.2-Antigen in diesen Populationen vorhanden war, während das Ly-1.1-Allel fehlte. Wie bereits bekannt, können beide Allele zwar nicht als Marker für die verschiedenen *Mus*-Taxa dienen, sie ermöglichen jedoch Informationen über den Genaustausch zwischen Populationen.

Eine polymorphe Verteilung der anderen untersuchten Antigene wurde angegeben und mit anderen Populationen von europäischen *M. m. domesticus* verglichen.

Aus immunologischer Sicht kann die systematische Stellung der untersuchten Populationen als *M. m. domesticus* bestätigt werden. Das steht in Einklang mit neueren Auffassungen, wonach die Rb-Populationen von *Mus* fast ausschließlich zu diesem Taxon gehören.

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Genic divergence in *Spalacopus cyanus* (Rodentia, Octodontidae)

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Abstract

Studied electrophoretic variation of proteins encoded by 23 loci in four populations of *Spalacopus cyanus*. Mean polymorphism and heterozygosity were 18.5 % and 5.8 %, respectively. Low levels of interpopulational genetic differentiation were found ($\bar{S}$ = 0.93, $\bar{D}$ = 0.032). Fixation index indicated a considerable degree of demic structuration (FST = 0.273), contrary to the inference that *Spalacopus* forms extensive interbreeding populations. Levels of interpopulational allozymic differences do not support the niche-width variation hypothesis. The amount of genic variation depends on the degree of isolation between local populations. Isolation in turn is influenced by physiographic features and historical chance events, and is not correlated to the geographic distance per se.

Introduction

Allozymic polymorphisms in subterranean rodents are interpreted as the stochastic outcome of factors including historical events and population structure (Patton 1980; Patton and Smith 1989), or as an adaptive consequence stemming from natural selection (Nevo 1990; Nevo and Shaw 1972). Historical events associated with the breeding structure (Patton 1980), and evlutionary constraints imposed by the fossorial way of life (Nevo 1979; Savic and Nevo 1990) have been invoked to explain the patterns of genetic variation in *Thomomys bottae* (Patton and Yang 1977), *T. umbrinus* (Patton and Feder 1978), and *Geomys bursarius* (Penney and Zimmerman 1976; Bohlin and Zimmerman 1982). Thus, gene flow is thought to be the causative agent responsible for patterns of genic and chromosomal variation as reflecting historical biogeography (Patton and Yang 1977). Alternatively, an adaptive strategy directed by natural selection operating in a monotonous subterranean niche has been proposed for *Spalax ehrenbergi* (Nevo and Shaw 1972), *Thomomys talpoides* (Nevo et al. 1974), and for the Bathyergidae (Nevo et al. 1987).

Subterranean *Spalacopus* is a monotypic genus of endemic herbivorous rodents (Contreras and Gutiérrez 1991) distributed throughout the western slope of the Andes of central Chile (Reise and Gallardo 1989a). Animals depict the same populational attributes (Reig 1970) and physiological adaptive syndrome (Contreras 1986) described for other underground mammals (Nevo 1979). Preliminary ecological studies in *Spalacopus* (Reig 1970) provided a basis for correlating the inferred wandering nature of the animals with karyotypic stability (Reig et al. 1972). In this study we examine the patterns of allozymic variation and degree of genetic fragmentation in four natural populations of *Spalacopus cyanus* from their coastal range. Low levels of interpopulation genetic differentiation as predicted by the high vagility attributed to *Spalacopus* are compared with electrophoretic data to test the consistency of such an ecology-based proposition.

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Material and methods

Electrophoretic analysis was carried out on 76 specimens belonging to four populations of *Spalacopus cyanus*. Sample designations, geographic coordinates, and number of specimens examined were as follows (Fig. 1): *Spalacopus cyanus cyanus*, Los Vilos (31° 55′ S, 71° 31′ W), 28; Los Cristales (31° 55′ S, 71° 29′ W), 7; Huentelauquén (31° 35′ S, 71° 32′ W), 10. *Spalacopus cyanus maulinus*, Quirihue (36° 17′ S, 72° 32′ W), 31. Voucher specimens were deposited in the Collection of Mammals, Institute of Ecology and Evolution, Universidad Austral of Chile.

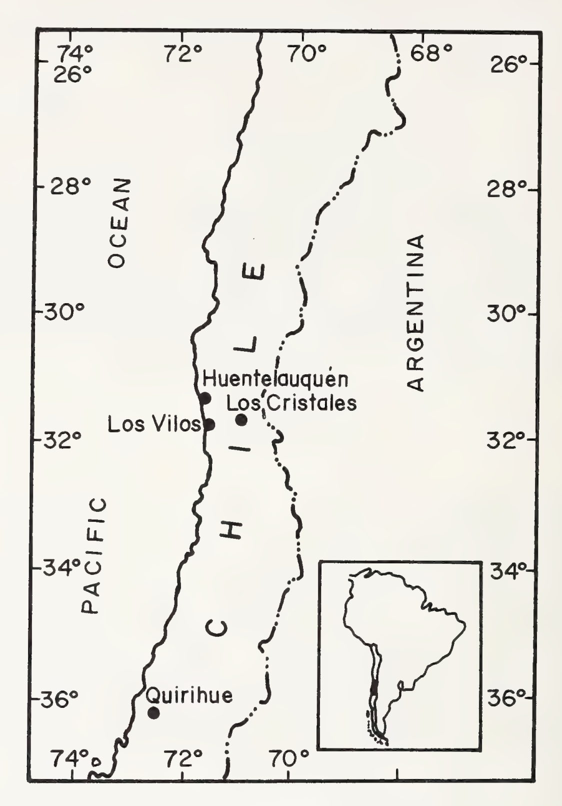


Fig. 1. Map of collecting localities of *Spalacopus cyanus*

Kidneys and liver were removed from each specimen and stored in liquid nitrogen after sacrifice. Homogenates, buffer systems, migration conditions, and mixtures for each system were prepared according to SELANDER et al. (1971). Fifteen enzymes and two non-enzymatic protein (albumin and transferrin) encoded by 23 presumptive genetic loci were examined. Details on the enzymes analysed, their tissue source, and electrophoretic procedures used are given in Table 1. Allozymes were named alphabetically according to their mobility relative to the commonest allele. A locus was considered polymorphic if the frequency of the most common allele did not exceed 0.95. D-statistics were computed to test for deficiency or excess of heterozygosity (SWOFFORD and SELANDER 1989). NEI's (1978) unbiased distance (D) and ROGERS' similarity (S) coefficients (ROGERS 1972) were calculated to compare pairs of samples. The genetic relationships among populations were represented by a dendrogram, using the weighted and the unweighted pair-group cluster algorithm (SNEATH and SOKAL 1963). An analysis of heterogeneity between pairs of populations was conducted by a contingency table using the Pearson chi-square statistic (SWOFFORD and SELANDER 1989). Spatial correlation in allele frequencies was examined by three distribution-free permutational approachs (MANTEL, KENDALL and SPEARMAN) that compare genetic and geographic distance matrices (DIETZ 1983).

Population subdivision was assessed through WRIGHT's F-statistics (WRIGHT 1965). All computations were performed in Biosys-1 (SWOFFORD and SELANDER 1989). The criterion of SLATKIN (1981) for minimum sample size (n = 10) was used to correct sampling bias of FST.

Table 1. **Enzymes, tissue sources and electrophoretic conditions resolved in *Spalacopus cyanus***

Enzyme	Enzyme commision number	Locus abbreviation	Electrophoretic conditions and tissue source[1]
Isocitrate dehydrogenase	1.1.1.42	ICD-1	4 (K)
	1.1.1.42	ICD-2	4 (K)
Malate dehydrogenase	1.1.1.37	MDH-1	4 (K)
	1.1.1.37	MDH-2	4 (K)
Glutamate-oxaloacetate transaminase	2.6.1.1	GOT-1	5 (L)
	2.6.1.1	GOT-2	5 (L)
Glycerol-3-phosphate dehydrogenase	1.1.1.8	GPD	5 (L)
Glucose 6-phosphate dehydrogenase	1.1.1.49	Gd	6 (K)
Lactate dehydrogenase	1.1.1.27	LDH-1	3 (K)
	1.1.1.27	LDH-2	3 (K)
Xanthine dehydrogenase	2.7.1.1	XDH	3 (K)
Glucose phosphate isomerase	5.3.1.9	GPI	7 (L)
Phosphoglucomutase	2.7.5.1	PGM-2	7 (L)
	2.7.5.1	PGM-3	7 (L)
Phosphogluconate dehydrogenase	1.1.1.44	PGD	7 (L)
Alcohol dehydrogenase	1.1.1.1	ADH-1	9 (L)
	1.1.1.1	ADH-2	9 (L)
Hexokinase	2.7.1.1	HK	9 (L)
Malic enzyme	1.1.1.40	ME-1	5 (L)
	1.1.1.40	ME-2	5 (L)

[1]from Selander et al. (1971). Tissue source (L) = liver, (K) = kidney.

Results

Eight of the 23 loci analyzed (GOT-1, TRFER, PGI-2, PGM-2, PGM-3, ADH-1, ADH-2, HK) were polymorphic in one or more populations whereas the remainder were monomorphic across all populations (Tab. 2). Four of the variable loci (GOT-1, PGM-2, PGM-3, ADH-2) were monomorphic in two or three populations.

The average number of alleles per locus ranged from 1.1 (Quirihue) to 1.3 (Huentelauquén and Los Vilos). Polymorphism per population fluctuated from 8.7 % (Quirihue) to 26.1 % (Los Vilos), with 19.6 % for overall polymorphism across all populations. Direct-count heterozygosity per population ranged from 0.6 % (Quirihue) to 7.3 % (Los Vilos), with an unweighted mean across all samples of 4.5 %.

D-statistics indicated a deficiency of heterozygotes in loci PGM-3 and ADH-1, and total absence of heterozygotes in loci GOT-1, PGI-2, and ADH-2, suggesting that some populations are influenced by nonrandom mating and small effective population sizes (Barrowclough 1980). Fixation of otherwise polymorphic alleles (GOT-1, TRFER, PGM-2, PGM-2, ADH-1) was observed in the Quirihue sample.

High values of genetic similarity, ranging from 0.972 (Los Cristales – Los Vilos) to 0.900 (Quirihue – Huentelauquén) were found. The genetic distance ($\bar{X}$ = 0.032) ranged from 0.001 (Los Vilos – Huentelauquén) to 0.074 (Quirihue – Huentelauquén). The non-significant results ($P \geq 0.079$) otained in the tests of association between geographic and genetic distance matrices indicated a nearly random distribution of genotypes (Epperson and Allard 1989).

The UPGMA and the WPGMA phenetic clustering procedures using genetic distances gave similar results, identifying two genetic subgroups (Fig. 2). The first was formed by the three northern samples, with Los Vilos and Los Cristales depicting the closest affinity. The second group was formed by the Quirihue sample, removed from the rest by the fixation of specific alleles (TRFER, ADH-1) that were polymorphic in the other samples

Table 2. **Allele frequencies of eight variable loci of four populations of *Spalacopus cyanus***

Locus	Population			
	Quirihue (N = 31)	Los Vilos (N = 28)	Los Cristales (N = 7)	Huentelauquen (N =10)
GOT-1				
A	.000	.036	.000	.000
B	1.000	.964*	1.000	1.000
TRFER				
A	.000	.481	.214	.300
B	1.000	.519	.786	.700
PGI-2				
A	.000	.000	.000	.300
B	.516	.179	.143	.300
C	.484*	.821*	.857*	.400*
PGM-2				
A	1.000	.679	.786	.100
B	.000	.321	.214	.900
PGM-3				
A	.000	.054	.071	.000
B	1.000	.946*	.929	1.000
ADH-1				
A	.000	.685	.643	.800
B	1.000	.315*	.357	.200
ADH-2				
A	.000	.036	.000	.000
B	1.000	.964*	1.000*	1.000
HEXOK				
A	.065	.107	.000	.100
B	.935	.893	1.000	.900

* Significantly different from the Hardy-Weinberg equilibrium.

(Tab. 1). The test for genetic heterogeneity between populations indicated significant differences between every pair of populations except Los Vilos and Los Cristales ($P \leq 0.37$), which were considered homogeneous by the test.

The mean FST was 0.273, indicating extensive genetic subdivision, despite the low genetic distances recorded. This means that 27 % of the total variance in allelic frequencies is expressed between the populations (Zink and Winkler 1983). If the Quirihue sample is removed from the analysis, maximum variance in allele frequency drops to FST = 0.140. Since an inverse correlation exists between Nm and FST, this indicates that an average of one individual every second generation is exchanged among populations (Hartl and Clark 1989). The inbreeding coefficient (FIS = 0.307) permitted examination of within-population breeding structure (van den Bussche et al. 1987). Negative FIS values were obtained for TRFER, PGM-2, and HK, reflecting fewer homozygous than expected under random mating (Chesser 1983; Ryman et al. 1980).

Discussion

These samples show levels of genetic variation typical of fossorial rodents (Nevo 1979). Mean heterozygosity and polymorphism are within the ranges obtained in *Geomys tropicalis* (Bohlin and Zimmerman 1982), *Thomomys umbrinus* (Hafner et al. 1987), and *Thomomys talpoides* (Nevo et al. 1974).

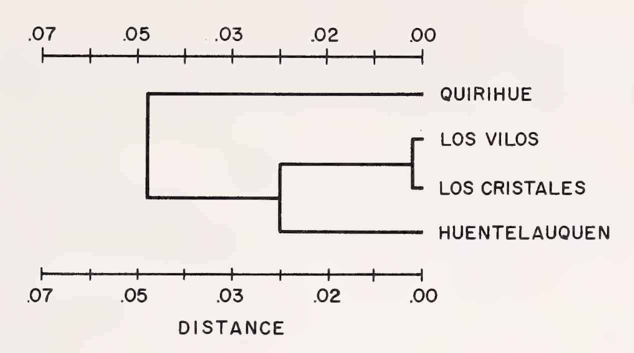


Fig. 2. Distance phenogram between populations of *Spalacopus cyanus*. The unweighted pair-group algorithm was used to cluster NEI's genetic distances (NEI 1978). Cophenetic correlation coefficient: 0.80

Low H has been invoked to be an adaptive strategy in the relatively uniform subterranean environment (NEVO 1990; NEVO and SHAW 1972). Although a regime of "homoselection" could be claimed for the excess of monomorphic loci in the Quirihue population, interpopulation genic differentiation argues against this explanation. If environmental heterogeneity alone were sufficient to maintain genetic variability, the same alleles under the niche-width hypothesis should be promoted by directional selection in all populations, regardless of distance (PATTON and FEDER 1978). High levels of homozygosity and low levels of polymorphism in the Quirihue sample are better explained as stemming from founder events affecting a geographical isolate where a decrease in the frequency of heterozygotes is expected to occur. A similar effect, but due to a small sample size is observed in the Huentelauquén sample where extensive inbreeding increases homozygosity while the genus' colonial behavior further reduces the effective population size (REISE and GALLARDO 1989b). This results in a pattern that mimics homoselection, especially in loci segregating at frequencies close to zero or one (GALLARDO and KÖHLER 1992).

Gregarious *Spalacopus* occupies a common burrow, establishing large populations formed by many small, nomadic colonies where no less than three generations coexist (REIG 1970). This nomadic behavior is thought to be a consequence of their herbivory, limited to bulbs of geophytes (REIG 1970). From these observations, high vagility has been inferred, and a concomitant enhancement of gene flow is expected to occur. Accordingly, chromosome uniformity and low taxonomic diversification are explained by the animal's feeding behavior (REIG et al. 1972). Nevertheless, diet resources are not depleted by feeding activities; on the contrary, bulb regeneration seems to be facilitated through seed germination suggesting coevolution of geophytes and *S. c. cyanus* (CONTRERAS and GUTIÉRREZ 1991). A similar feeding dynamic was observed in *S. c. maulinus* feeding on *Dioscorea longipes*. Here, regermination induces a recurrent pattern of revisiting old dwelling areas, reversing the animals' nomadic habitus, thus arguing against high vagility (REISE and GALLARDO 1989b). Apparently, genetic drift plays a significant role in shaping the genetic structure of these populations. As the effective population size is small, local extinctions and concomitant erosion of the genetic variation by historical bottlenecks are likely to occur (MARUYAMA and FUERST 1985; WADE and MCCAULEY 1988).

These *Spalacopus* populations occur in descrete patches where the dynamics of finite populations involve the internal demographic potential (LANDE 1987) and external factors stemming from habitat fragmentation (HASTINGS and WOLIN 1987; HANSKI 1991). Accordingly, it seems that gene flow is efficient to maintain genetic integrity only in short distances where habitat continuity and the distribution of suitable soil types allows it. On a larger geographic scale, interpopulation genetic cohesion is affected by chance events

related to physiographic features (Reise and Gallardo 1989a). Thus, long distance gene flow is affected by stochastic events acting in a long-term historical scale within finite populations, and thus may not be correlated at present with actual distances (Patton and Yang 1977).

Acknowledgements

We thank Corporación Nacional Forestal and Servicio Agrícola y Ganadero for providing collecting permits. Field work assistance was provided by R. Aros, F. Mondaca and D. Reise. This research was partially funded by Fondo Nacional de Ciencias, Grant 92–178, and Dirección de Investigación y Desarrollo, Universidad Austral de Chile, Grant S-91-11 to MHG.

Zusammenfassung

Genetische Divergenz bei Spalacopus cyanus (Rodentia, Octodontidae)

Die elektrophoretisch ermittelte Proteinvariation von 4 Populationen von *Spalacopus cyanus* ließ sich in 23 Loci kodifizieren. Mittlerer Polymorphismus und mittlere Heterozygose betrugen 18,5 % bzw. 5,8 %. Es wurde ein geringer Grad an interpopulationärer genetischer Differenzierung gefunden (S = 0,93; D = 0,032). Der Fixierungs-Index zeigte im Gegensatz zur Annahme, daß bei *Spalacopus* extensive Durchmischung vorherrscht, ein beträchtliches Ausmaß an demischer Strukturierung (FST = 0,273). Der Grad allozymischer interpopulationärer Differenzen stützt nicht die Hypothese der Variation von Nischen-Weiten. Das Ausmaß an genetischer Variation beruht auf dem Isolationsgrad zwischen lokalen Populationen. Isolierung ist durch physiographische Gegebenheiten und historische Chancenereignisse beeinflußt und ist nicht mit der geographischen Distanz per se zu korrelieren.

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The population dynamics of rodents at Settlers, Transvaal, South Africa

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Abstract

Studies of populations of *Mastomys natalensis* and *Rhabdomys pumilio* have shown that densities increased in late summer and peaked in midwinter. Numbers were low in spring over midsummer. Small numbers of *Otomys angoniensis* were caught throughout the year. Breeding in *M. natalensis* ended in March–April and recommenced in August–September. Breeding in *R. pumilio* ended in May and recommenced in August. Reproductively active adult *O. angoniensis* individuals were present throughout the year. There was a small peak in juvenile numbers of *M. natalensis* and *R. pumilio* in spring, but little juvenile recruitment over midsummer. The mean body mass of *M. natalensis* and *R. pumilio* declined from a peak in March to low values throughout the winter, followed by a slight increase in spring. The body mass of *O. angoniensis* was highly variable. The low numbers of *O. angoniensis* caught are ascribed to trap-shyness rather than low density in the field. *O. angoniensis* was probably present in fairly high numbers throughout the year.

Introduction

Rodent population census, by trapping, has been done extensively at various localities in South Africa, but usually at monthly intervals, or longer. In order to ascertain possible subtleties in rodent demography, trapping was instituted weekly. A prior study by Mendelsohn (1982a) found three common rodent species, the multimammate mouse *Mastomys natalensis*, the fourstriped field mouse *Rhabdomys pumilio*, and the angoni vlei rat *Otomys angoniensis* to be resident on the study area at Settlers. This paper deals with the demography of the rodent populations in relation to season and body mass dynamics.

Material and methods

The study site was situated near Settlers (24° 57′ S, 28° 33′ E) on the Springbok Flats, Transvaal, South Africa. This study area fell inside that of Mendelsohn (1982a, b). The topography was flat, but drainage lines produced a gently rolling landscape from East to West. The area was used for mixed farming, with cultivated fields (72 %) interspersed with patches of grazed bushveld (27 %). The entire area was on Springbok Flats Turf Thornveld (Acocks 1975). The rainfall data (Fig. 1) were obtained from Deeside farm, on the southern edge of the study area.

Mastomys natalensis has been separated into sibling species (*M. natalensis* and *M. coucha*) based on chromosome numbers and haemoglobin electrophoresis (Bronner 1986; Green et al. 1980; Meester et al. 1986). Meester et al. (1986) do not give the Springbok Flats (Northern Transvaal) in the distribution of either species. As the *M. natalensis* population at Settlers was not identified to sibling-species level, we will use *M. natalensis* as referring to *M. natalensis* sensu lato throughout.

Two live-trap lines were established, the first (Line A) through grazed bushveld on black turf [Mendelsohn's (1982a) line 2]. This line crossed a dry river bed which was later flooded. The second (Line B) ran along a fence between a tarred road (5 m away) and a cultivated field (5 m away). This line incorporated both black turf as well as red clay [Mendelsohn's (1982a) lines 4 and 5]. Trapping was initiated in February 1986, and in June 1986 the number of traps was increased from 20 to 35 in line A and from 20 to 40 in line B. Both lines were set weekly, for two trapping nights per week. The

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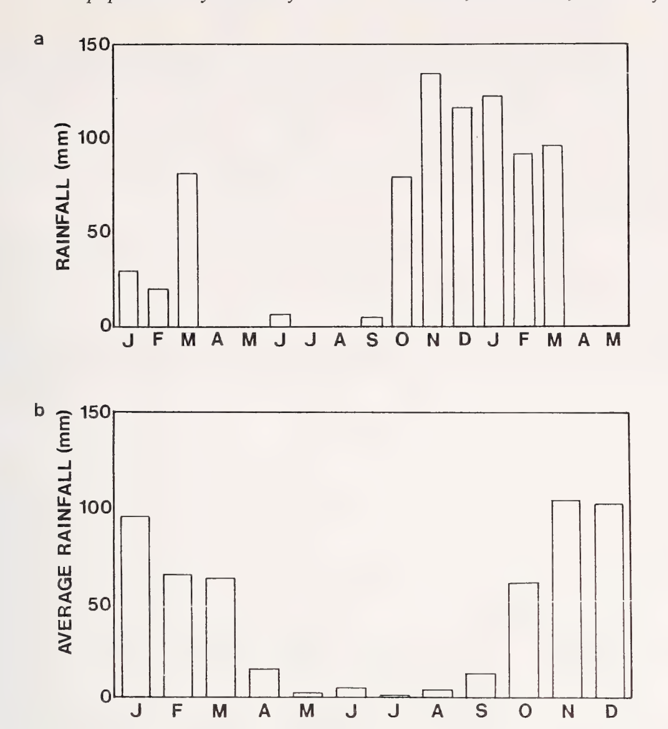


Fig. 1. Rainfall figures at Deeside Farm on the southern border of the study area. a: Rainfall during the study period. b: Average rainfall from 1978 to 1987

traps were placed 6 m apart, adjacent to runways or other signs of rodent activity (to increase the capture rate of *O. angoniensis*). The traps were baited with peanut butter and oats, and left in place throughout the study period. From February to May 1986 all animals caught were removed, but from mid-June 1986 capture-mark-recapture (Flowerdew 1976) was instituted, using the toe-clipping method (Twigg 1875a).

Additional trapping was done using snap-traps, placed randomly along a field verge between two cultivated fields [on black turf (Mendelsohn 1982a, line 4)]. These traps provided data on population age and sex structures, and body mass.

All animals were identified, aged, sexed, weighed, and their reproductive condition noted. Reproductively active individuals were defined as those that were scrotal (males), or that were perforated, pregnant or lactating (females) (Twigg 1975b). Body mass was used to separate individuals into juvenile and adult age classes, with the separating mass being: *M. natalensis* – 30 g (David and Jarvis 1983); *R. pumilio* – 30 g (Brooks 1974, 1982; David and Jarvis 1985) and *O. angoniensis* – 50 g (Davis 1973). Individuals which showed reproductive activity although weighing less than the above values, were considered to be adults.

Two indices of population numbers were obtained: a. the minimum number of mice alive (MNA) (David and Jarvis 1985) [MNA = the number of mice actually caught + the number of mice marked before the Ith trapping occasion, which were not caught at the Ith occasion but were captured subsequently (i.e. mice assumed to have been present at time I)]. b. As the number caught per 100 trap-nights (1 trap night = 1 trap set for 24 hours) (Chidumayo 1984; Mendelsohn 1982a).

Results

Three species dominated the captures: *Mastomys natalensis*, *Rhabdomys pumilio* and *Otomys angoniensis*. Occasionally shrews (*Crocidura* spp. n $<$ 20), the striped mouse *Lemniscomys rosalia* (n = 2) and the pouched mouse *Saccostomus campestris* (n = 1) were caught. The results focus on the first three species.

Population numbers

Numbers of *M. natalensis* (Fig. 2a, b) increased from February to the end of June, and then gradually decreased over late winter. There was a slight peak in late spring, low numbers over midsummer, and an increase towards the end of summer (Fig. 2.1b). The MNA showed fairly constant numbers over winter, a slight increase in late spring and a decrease over midsummer.

Fewer *P. pumilio* were caught (Fig. 3a, b) than *M. natalensis*. *R. pumilio* showed the same seasonal trend in numbers as *M. natalensis*, with the exception of the spring peak. No *R. pumilio* were trapped after the end of October.

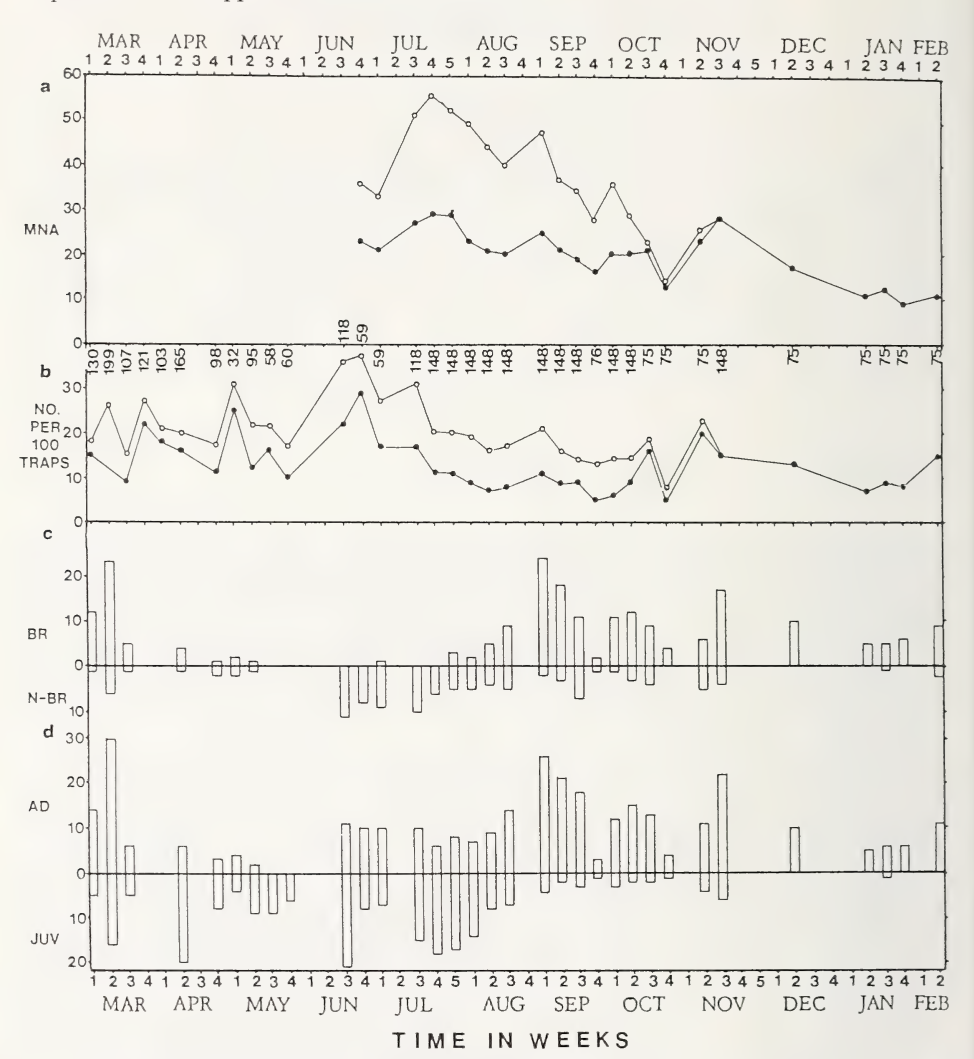


Fig. 2. The population demography of *Mastomys natalensis* at Settlers during the study (see text for details). a: The minimum number of mice alive (MNA) through the study period. b: The number of individuals caught per 100 trap nights through the study period. c: Breeding season: the number of adult individuals in breeding (BR) and non-breeding (N-BR) condition. d: Age structure: the number of adults (AD) and juveniles (JUV) present, ○—○ = all species trapped; ●—● = *M. natalensis.* Numbers between a and b indicate the number of traps used in each trapping session

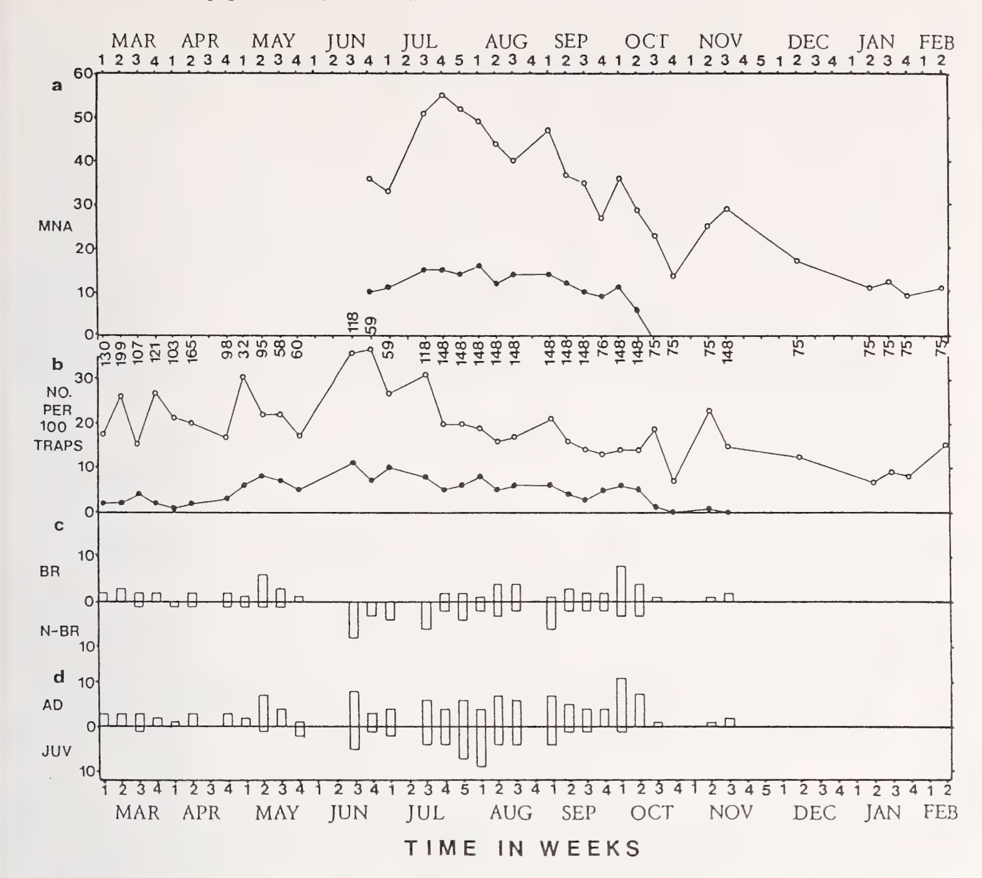


Fig. 3. The population demography of *Rhabdomys pumilio* at Settlers during the study (see text for details). a: The minimum number of mice alive (MNA) through the study period. b: The number of individuals caught per 100 traps nights through the study period. c: Breeding season: the number of adult individuals in breeding (BR) and non-breeding (N-BR) condition. d: Age structure: the number of adults (AD) and juveniles (JUV) present. ○—○ = all species trapped; ●—● = *R. pumilio*. Numbers between a and b indicate the number of traps used in each trapping session

Breeding season

The breeding season of *M. natalensis* came to an end in March–April, with few reproductively active animals caught from June to July (Fig. 2c). Breeding began again in August–September and reproductives were present throughout spring and summer. Seasonal changes in recruitment (juveniles present – Fig. 2d) showed a slight peak in numbers in November, and an absence of juveniles from December to February.

Although present data for *R. pumilio* are not as complete as for *M. natalensis,* indications are that reproductive activity ceased in May, and recommenced in August (Fig. 3c). Juvenile numbers increased over winter, but there were no juveniles trapped in spring (Fig. 3d).

Reproductively active *O. angoniensis* adults were present throughout the year, showing no marked breeding season (Fig. 4c). Very few juveniles were trapped, but indications were that juveniles were born throughout the year (Fig. 4d).

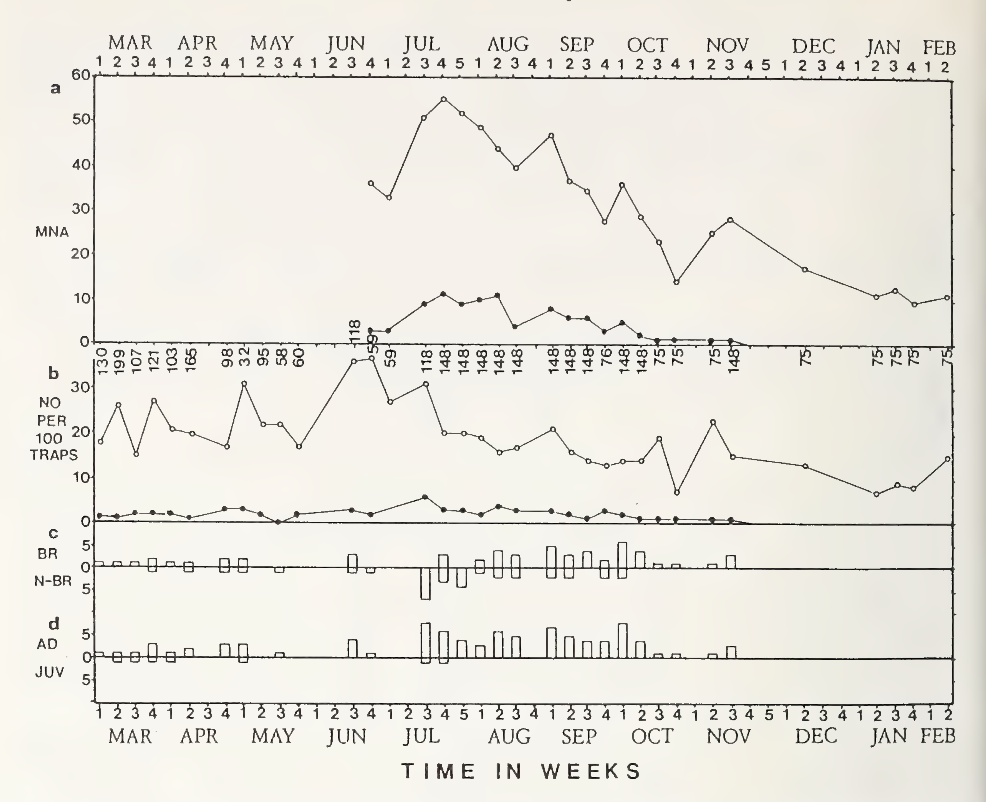


Fig. 4. The population demography of *Otomys angoniensis* at Settlers during the study (see text for details). a: The minimum number of mice alive (MNA) through the study period. b: The number of individuals caught per 100 traps nights through the study period. c: Breeding season: the number of adult individuals in breeding (BR) and non-breeding (N-BR) condition. d: Age structure: the number of adults (AD) and juveniles (JUV) present. ○—○ = all species trapped; ●—● = *O. angoniensis*. Numbers between a and b indicate the number of traps used in each trapping session

Body mass

Mean body mass of *M. natalensis* is shown in Figure 5a, while that of adults and juveniles are shown separately in Figure 5b. Adult body mass (Fig. 5b) was low over winter, and then increased from spring onwards to a peak in January–February. The mass of juveniles increased through autumn to relatively high levels in spring, as they matured.

The mean body mass of *R. pumilio* (Fig. 6b) decreased from a peak in March to lower values throughout winter, and then increased slightly in spring. Body mass of *O. angoniensis* was highly variable throughout the period illustrated (Fig. 6a).

Discussion

The correlation between rainfall and the seasonality of reproduction in many African grassland rodents is generally accepted. Leirs et al. (1989) in a detailed, three year study of *M. natalensis* at Morogoro, Tanzania, have shown that the breeding season starts soon after the onset of the rainy season in March–April, but if rainfall at the end of the year is heavy, there is a short additional separate breeding period early in the following year.

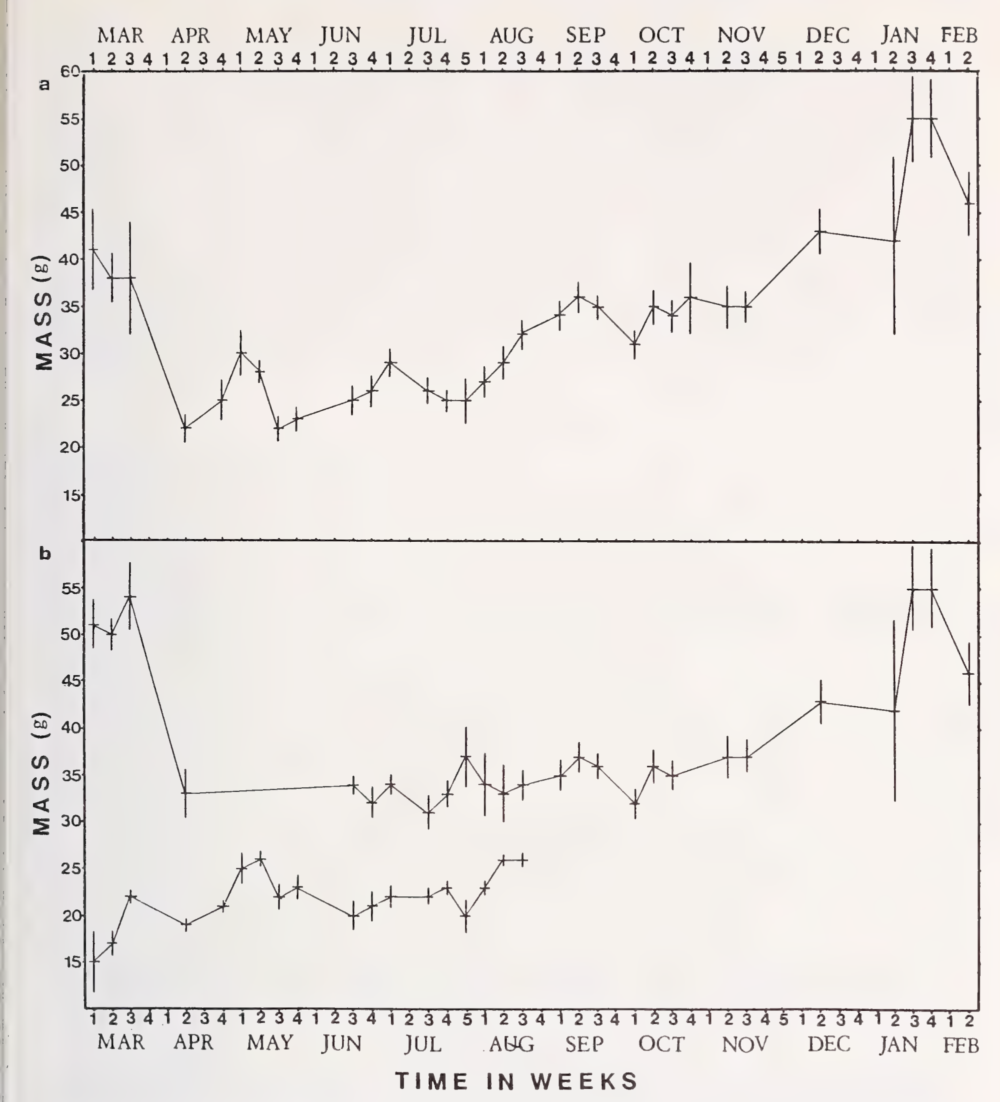


Fig. 5. The body mass of *Mastomys natalensis* at Settlers during the study. a: The body mass of all individuals from each trapping session pooled. b: The body mass of adult and juvenile individuals shown separately. Horizontal lines indicate means; and vertical lines indicate 1 X SE error

Population numbers

M. natalensis numbers at Settlers follow closely the trend found in the same area by Mendelsohn (1982a). Chidumayo (1984) also found a small increase in late spring followed by lower numbers from November to December. Unfortunately his trapping ended in December. Mendelsohn (1981) ascribed the small spring peak in numbers to the production of juveniles, and the low midsummer numbers to low rates of juvenile recruitment. This is supported by this study which showed an increase in the number of juveniles at the time of the spring peak, followed by an absence of juveniles over midsummer.

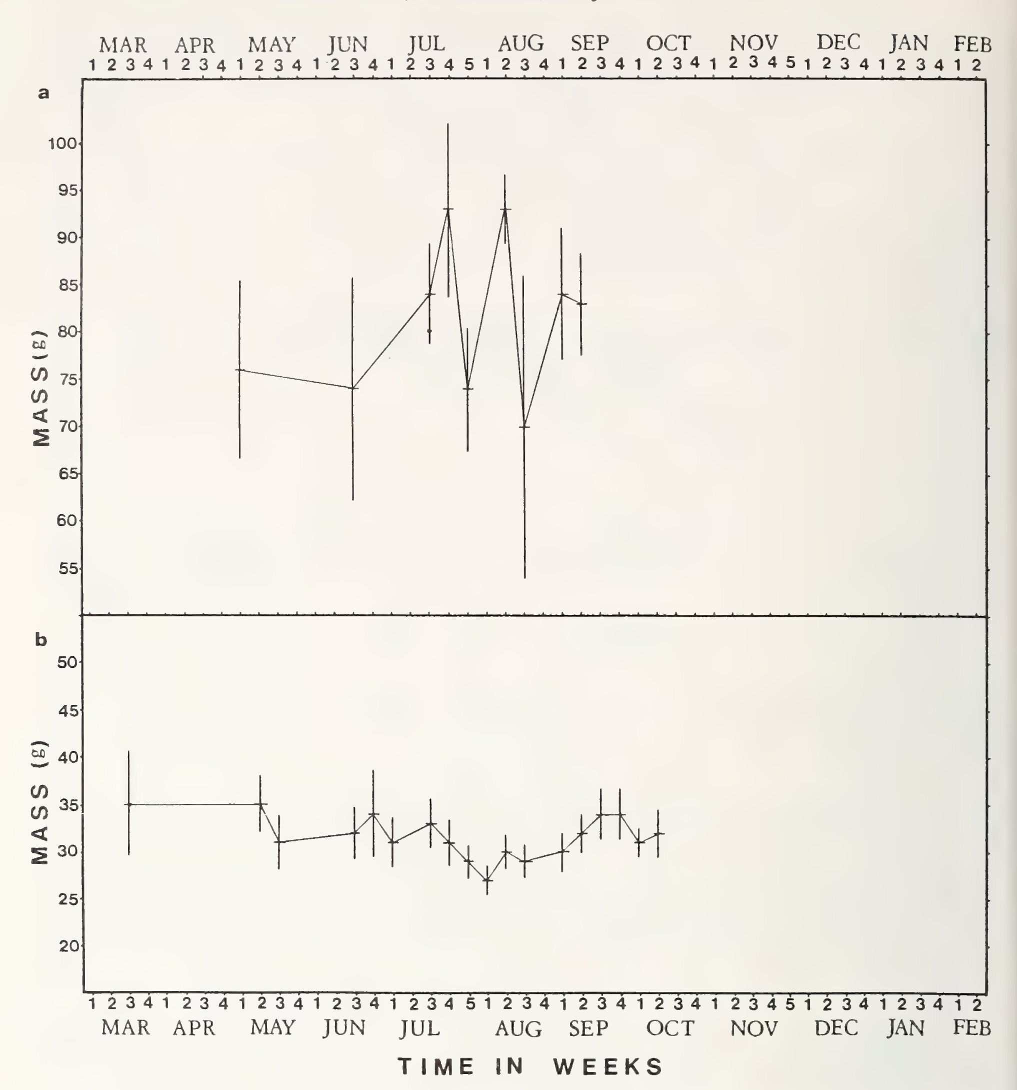


Fig. 6. The body mass of *Rhabdomys pumilio* and *Otomys angoniensis* populations at Settlers during the study. a: The body mass of *Otomys angoniensis* individuals. b: The body mass of *Rhabdomys pumilio* individuals. Horizontal lines indicate means; and vertical lines indicate 1 X SE error

A possible reason for the low numbers over midsummer is the large amount of rain which fell at Settlers from late October through to the end of January. TAYLOR and GREEN (1976) suggest that exceptionally heavy or prolonged rainfall results in very successful reproduction. This would, however, be a longterm effect, the immediate effect perhaps being a decrease in numbers (because of flooding). Individuals may die from overnight exposure when wet (PERRIN 1975), or the decrease in numbers may be because animals moved out of the flooded areas.

R. pumilio numbers were similar to those of MENDELSOHN (1982a), who also found that population numbers were lowest from November to February. BROOKS (1974) showed an increase in *R. pumilio* from May to June, followed by a gradual decrease, with lowest numbers in mid-summer. He trapped in an intensive grid, and the number of animals

trapped per session ranged from a minimum of 40 upward. His results may well be indicative of the trends in the whole Transvaal population, as corroborated by this study and MENDELSOHN (1982a). DAVID and JARVIS (1985), working in the western Cape (winter-rainfall area) found that numbers began to increase from October to November, and rose steadily to a peak in February–March; this was followed by a decline during winter, with lowest numbers in August–September. The general trend was therefore the same as in the Transvaal, but with the cycle shifted three months earlier.

DAVIS (1973) found that *O. angoniensis* numbers were constant from March to December of one year, followed by an increase over the next year to a peak in November. This was followed by a decrease. *O. angoniensis* numbers seem to lack the seasonal fluctuations shown by of the other two species, and rather display relatively constant numbers that vary yearly rather than seasonally.

Breeding season

MENDELSOHN (1982a) found a similar breeding season to this study, with reproductives appearing from July to September, and juveniles showing a slight peak in numbers in September, before very low numbers over summer. He suggested that this was a result of an interrupted breeding season, in which young are produced in spring and late summer-autumn. He found, as in this study, that reproductives were present throughout the summer, and suggested that the absence of juveniles was because environmental conditions were not suitable for the production and/or survival of young. The work of CHIDUMAYO (1984) and TAYLOR and GREEN (1976) agrees with the current results and MENDELSOHN's (1982a, b) data. COETZEE (1965), however, showed that pregnant females are present in large numbers from September onwards (throughout the summer), with 44 % of the adult females caught in December being pregnant. It seems therefore that the *M. natalensis* populations attempt to breed continuously from August to March, but juvenile mortality limits recruitment over midsummer.

The absence of spring recruitment in *R. pumilio* could have been because unusually high rainfall from October to January caused high juvenile mortality. MENDELSOHN (1982a) showed the *R. pumilio* breeding season to be similar to that of *M. natalensis*. PERRIN (1980) showed a recession in breeding over midsummer, and attributed this to an environmental factor (drought). ROWE-ROWE and MEESTER (1982) found reproductives present from September to March. Their results also indicated a drop in recruitment in November. The first young entered the trappable population in October, but no juveniles were captured during November. No trapping was done in December, and they trapped juveniles from January onwards. DAVID and JARVIS (1985) showed numbers of reproductives increasing in September, and present until March; juveniles increased from November through to May. This disagrees with the above findings, but they worked in a winter-rainfall area. Survival of young would depend on environmental conditions, and in certain areas (e.g. Settlers) survival may be adversely affected over midsummer, as is the case with *M. natalensis*.

As in our study, TAYLOR and GREEN (1976) found pregnant *O. angoniensis* females throughout the year, with a breeding peak in the wetter months. They found that the number of juveniles trapped varied little. *O. angoniensis* therefore shows little seasonality in reproduction, other than a slight peak in wet months (summer).

Body mass

The decrease in *M. natalensis* adult body mass over winter is documented by several authors (CHIDUMAYO 1984; COETZEE 1965; TAYLOR and GREEN 1976). Growth and maturation seem therefore to be delayed over winter, juveniles not becoming mature until spring.

R. pumilio body mass changes were similar to those of *M. natalensis.* This trend is supported by HENSCHEL et al. (1982) and TAYLOR and GREEN (1976) who suggest that growth and maturation are inhibited during the non-breeding season (winter).

The body mass of *O. angoniensis* varied greatly at each trapping session, and small sample sizes probably disguised trends. DAVIS (1973) found that *Otomys irroratus* lost mass over winter.

General

Numbers of *M. natalensis* and *R. pumilio* peaked in autumn following summertime breeding, but recruitment occurred after the summer rains, when body masses were high. Although adults were reproductively active throughout summer, density did not increase. This apparent paradox has been recorded previously but not adequately explained. It has been inferred that low juvenile recruitment, or infant mortality, is caused by environmental factors, including heavy rainfall (TAYLOR and GREEN 1976), drought or nutrition (PERRIN 1980). However, temporal correlations between environmental variables and demographic events may not be indicative of cause-effect relationships and alternative explanations should be considered.

Changes in the survival and recruitment of young into natural murid populations have been explained by intraspecific competition in the form of aggression (SADLEIR 1965; HEALEY 1967; WATTS 1969). For example, the mortality of young redbacked voles *Clethrionomys grapperi* is greatest during the summertime breeding season, when levels of aggression are higher in adults than young (PERRIN 1981) and when diet is optimal and body growth is greatest (PERRIN 1979). Field experiments, that manipulate density (and hence aggression) and food resources (independently of climate) while agonistic behaviour is being monitored and quantified, are necessary to distinguish between alternative explanations of demographic process. Descriptive studies of the population dynamics of African rodents should now be complemented with experimental investigations.

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Zusammenfassung

Die Populationsdynamik von Nagetieren in Settlers, Transvaal, Südafrika

Studien über Populationen von *Mastomys natalensis* und *Rhabdomys pumilio* haben ergeben, daß ihre Dichte zwischen Februar und Ende Juni zunahm und in der Mitte des Winters wieder abnahm. Im Frühling gab es ein Populationsmaximum, das während des Hochsommers abnahm. *Otomys angoniensis* konnte ganzjährig in kleinen Zahlen gefangen werden. Die Wurfzeit von *M. natalensis* kam im März/April zum Abschluß und begann wieder im August/September. Die Wurfzeit von *R. pumilio* endete im Mai und fing im August wieder an. Fortpflanzungsfähige, ausgewachsene *O. angoniensis* kamen das ganze Jahr über vor. Die Zahlen der Jungtiere von *M. natalensis* und *R. pumilio* erreichten im Frühling ihr Maximum; wenige Jungtiere ergänzten die Populationen während des Sommers. Karge Umweltbedingungen könnten die Überlebenschancen der Jungtiere im Sommer beeinträchtigt haben. Das Durchschnittskörpergewicht von *M. natalensis* und *R. pumilio* nahm ab von einem Maximum im März bis zu geringen Werten im Winter. Im Frühling gab es eine kleine Gewichtszunahme. Das Körpergewicht von *O. angoniensis* variierte stark. Die niedrige Zahl von gefangenen *O. angoniensis* wird eher der Fallenscheu zugeschrieben, als daß sie die tatsächlichen Populationsverhältnisse widerspiegelt.

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Cytogenetics and fossil record: confluent evidence for speciation without chromosomal change in South American canids

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South American wild dogs and foxes are the most diversified canids of any other continent, including seven genera and 11 species distributed in a wide range of habitats of the Neotropics (Berta 1987). However, this group is the least known of the Canidae in many aspects of its general biology. The South American fox, *Dusicyon* (Honacki et al. 1982) or *Pseudalopex* (Berta 1987), is the most polytypic genus encompassing five living species among which the chromosomes have only been reported for *D. vetulus* from Brazil (Wurster and Benirschke 1968). In this note we describe the karyotypes of two other species of *Dusicyon*, the Patagonian red fox, *D. culpaeus*, and the Pampean gray fox, *D. gymnocercus*. Moreover, we discuss the trends in chromosomal evolution of South American Canidae in conjunction with available information on fossil records.

Cytogenetic analysis was performed in four *D. culpaeus* from the breeding stock of piros sa, Argentina (1 male and 1 female) and from the Zoo of Buenos Aires City (2 females), and in three *D. gymnocercus* (1 male and 2 females) maintained at the Zoo of Buenos Aires City. Chromosomes were obtained from blood culture. In brief, blood samples were aseptically taken with heparanized syringes from the cephalic vein of the foreleg. One ml of whole blood was cultured in Eagle Minimun Essential medium supplemented with 20 % fetal calf serum, 2× glutamine, antibiotics (penicillin-streptomycin), and phytohemagglutinin. After 68 h at 37 °C, cultures were arrested with colchicine (1 µg/ml of culture) for 1.5 h. Colchicine-treated cultures were centrifuged at 1,000 rpm, resuspended in 0.075 M KCl for 15 min at 37 °C, and then fixed in cold 3:1, methanol:acetic acid. Chromosome spreads were air-dried and stained with Giemsa.

Both *D. culpaeus* and *D. gymnocercus* showed a 2n = 74 (NF = 76) karyotype, with an all-telocentric autosomal complement decreasing gradually in size, a large submetacentric X, and a small subtelocentric Y chromosome (see Figure). This karyotype is identical to that previously reported for the hoary fox, *D. vetulus* (Wurster and Benirschke 1968).

The South American canids evolved along two different lines (Langguth 1975): invading forest habitats and producing specialist forms such as *Atelocynus* and *Speothos*; or, colonizing the open plains as generalized species, e.g. of the genus *Dusicyon*. Both evolutionary lines have maintained the same 2n = 74–76 all-telocentric karyotype (Table).

Cerdocyon thous und *Urocyon cinereoargentus* are exceptions to the chromosomal homomorphism which characterizes the South American canids. *C. thous* also shows a 2n = 74 karyotype, but 36 metacentric and submetacentric autosomes which increase the number of arms up to 110 (Wurster-Hill 1973). The origin of this karyotype may be deduced by the accumulation of pericentric inversions in the all-telocentric karyotype. However, the required extent of such repatterning and the lack of known intermediate

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Giemsa stained karyotype of the Patagonian red fox, *Dusicyon culpaeus* (2n = 74, FN = 76). The same karyotype is also found in the Pampean gray fox, *D. gymnocercus*

states between the all-telocentric condition and *C. thous*-karyotype weaken this assumption. The karyotype of *U. cinereoargentus* (2n = 66; NF = 70) departs from the all-telocentric one, and may be derived by means of tandem fusions which reduce the diploid number without altering the number of arms, plus one pericentric inversion giving rise to the only metacentric autosome which characterizes this karyotype. Nevertheless, *U. cinereoargentus* is mainly distributed in North and Central America, reaching Colombia and Venezuela, and there are no fossil records in South America. This species probably represents a North American canid which reached the north of South America (Berta 1987).

Available chromosomal data in living species of South American Canidae

Species	2n	NF	Reference
Atelocynus microtis	74/76	76	Wurster and Benirschke (1968)
Cerdocyon thous	74	110	Wurster-Hill (1973)
Chrysocyon brachiurus	76	78	Newnham and Davidson (1966)
Dusicyon culpaeus	74	76	This study
D. griseus	?	?	
D. gymnocercus	74	76	This study
D. sechurae	?	?	
D. vetulus	74	76	Wurster and Benirschke (1968)
Speothos venaticus	74	76	Wurster and Benirschke (1968)
Urocyon cinereoargentus	66	70	Wurster and Benirschke (1968)

Fossil records indicate that the open plains of North America seem to have been the center of evolution of canids that later dispersed to South America (Berta 1987). A species or group of generalized canids entered South America after the emergence of the Panamian Land Bridge during the late Pliocene and early Pleistocene, and spread over the grasslands along the Andes reaching the southern pampas, the Patagonian grasslands, and the Brazilian highlands (Berta 1987; Langguth 1975). It is of interest to note that discrepancies in karyotype homomorphism mentioned above, are found in those genera for which earlier North American fossils are recorded – *Cerdocyon* and *Urocyon* – (Berta 1987). The

remaining canid species that radiated in South America – *Atelocynus, Dusicyon* and *Speothos* – display a high chromosomal conservatism. In addition, the all-telocentric karyotype of 74 chromosomes is also found in *Chrysocyon*, a form early recorded for North America and now restricted to a South American distribution.

Chromosomal information, in conjunction with fossil records seems to indicate that: 1. the species recorded early in North America which later attained South America, show a low karyological affinity with the other South American canids and are more closely related to the North American ones; this is the case for *C. thous* and *U. cinereoargentus*, 2. the 2n = 74 all-telocentric karyotype is most likely the primitive condition for South American Canidae, retained without change during diversification which resulted mainly from an opportunistic feeding strategy (Berta 1987), and 3. a North American origin may be suspected for this primitive karyotype which is also found in the early North American recorded genus *Chrysocyon*.

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Immobilization of Egyptian mongooses, *Herpestes ichneumon*, with a combination of ketamine and xylazine

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Based on three immobilizations, BELTRÁN et al. (1985) suggested that dosages of 7 mg per kilogram of body weight of a combination of ketamine hydrochloride (KE) and xylazine hydrochloride (XY), could be enough to successfully immobilize free-ranging Egyptian mongooses, *Herpestes ichneumon*. However, MADDOCK (1989) needed higher dosages (36 mg/kg on average) of KE to immobilize 22 individuals of this same species. These results suggest that BELTRÁN et al. (1985) could not have actually immobilized their mongooses, and that higher dosages of anaestetic should be administered for total immobilization. Here, we report the result of 48 total immobilizations of free-ranging Egyptian mongooses of different sex and age, using similar drugs and dosages to that of BELTRÁN et al. (1985).

Mongooses were captured between September 1987 and July 1989 with wire cage traps, cork double-door box for dens, or padded foothold traps (PALOMARES 1990). After the capture, mongooses were transported to the laboratory and moved into a box with a sliding wall that allowed us to inject intramuscularly a combination of KE (10 mg/ml; Ketolar) and XY (2 %; Rompun) into their hind quarters. An additional dose of KE, or KE and XY was administered when immobilization was only partial (SEAL and KREEGER 1987).

Induction time (time from injection until total immobilization) and arousal time (time from injection until first head, leg or mouth movement) were recorded for every individual. Rectal temperature records were taken as soon as practical after immobilization, and successive ones at 8–10 min intervals until handling procedures were completed.

We immobilized 26 different mongooses 48 times. We used mean dosages of 4.2 and 6.5 mg/kg of body weight of KE and XY respectively, irrespective of sex or age classes ($p > 0.05$; ANOVA; Table). Mean induction and arousal time were 7 and 74 min respectively (Table). Induction time and arousal time did not differ significatively among sex and age classes (Table). In 6 individuals, a mean dose of 3.9 mg/kg (SD = 0.7, range = 3.2–5.0) of KE and 6.0 mg/kg (SD = 0.9, range = 4.0–7.0) of XY was insufficient for total immobilization and complementary dosages of 2 mg/kg of KE and 2 mg/kg of XY were needed.

Rectal mean temperatures for the first, second, and third record were very similar (around 37.7 °C; Table). No difference was observed among classes of individuals (Table).

Three individuals were immobilized on 4, 4 and 6 occasions at intervals of 4, 8, and 1.6 months, respectively. One was immobilized twice in 24 hours. No animal died during the immobilization or recuperation processes, and we never observed spasms or convulsions with muscular contractions, as were sometimes noted in other carnivores (e. g. BOYD et al. 1990). Vomits were frequent during the recuperation.

We successfully immobilized mongooses using similar and lower dosages of KE than those used by BELTRÁN et al. (1985) and MADDOCK (1989), respectively. MADDOCK (1989) sometimes used Acetilpromacine as tranquilizer together with KE. Our results proved that a combination of KE and XY is an effective and safe immobilizing agent for Egyptian

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Ketamine hydrochloride (Ketolar) and tiazine hydrochloride (Xilacine) dosages (mg/kg) administered, induction time (Ind. time), arousal time (Arous. time), and three successive records of rectal body temperature (Temp. 1, Temp. 2, Temp. 3) for adult females, adult males and young (in this group we included the data of two immatures individuals) of Egyptian mongooses

ANOVA values and probabilities from comparisons among classes of individuals are given as well

	Ketolar	Xilacine	Ind. time	Arous. time	Temp. 1	Temp. 2	Temp. 3
Females							
Mean (SD)	4.2 (0.9)	6.8 (1.6)	7.0 (4.3)	67.7 (34.7)	37.7 (1.2)	37.2 (2.1)	37.6 (1.4)
Range	2.3–6.8	4.9–11.7	3–17	27–151	36.1–40.0	36.0–39.9	35.4–39.9
N	20	20	20	18	14	14	10
Males							
Mean (SD)	4.3 (1.5)	5.8 (1.6)	7.4 (3.5)	99.0 (36.7)	37.7 (1.1)	37.3 (1.4)	37.4 (1.7)
Range	3.2–7.8	3.5–8.9	5–16	47–107	36.2–39.8	36.1–40.0	35.5–39.1
N	9	9	9	9	7	7	5
Young							
Mean (S)	4.1 (0.7)	6.8 (1.6)	5.3 (2.3)	65.3 (29.7)	37.9 (1.1)	37.9 (1.2)	38.0 (1.0)
Range	2.3–7.8	3.5–11.7	3–10	16–120	35.4–39.2	35.1–39.2	36.3–39.1
N	13	13	12	12	10	10	8
Total							
Mean (SD)	4.2 (1.0)	6.5 (1.4)	6.8 (3.7)	74.2 (35.6)	37.9 (1.1)	37.6 (1.2)	37.7 (1.3)
Range	2.3–7.8	3.5–11.7	3–17	16–170	36.1–40.0	35.1–40.0	35.4–39.9
N	42	42	41	39	31	30	22
ANOVA (F)	0.160	0.941	1.162	3.185	0.181	0.276	0.760
Probability	0.085	0.399	0.323	0.053	0.835	0.761	0.480

mongooses. Some advantages with ketamine use as an anaesthetic in wild carnivores are described in Smuts and Bryden (1973).

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BUCHBESPRECHUNGEN

Penzlin, H.: **Lehrbuch der Tierphysiologie.** 5., durchgesehene Auflage. Jena: Gustav Fischer Verlag 1991. 657 S., 418 Abb., 75 Tab., kartoniert DM 58,–. ISBN 3-334-60363-6

Wenn ein Lehrbuch, welches 1970 erstmals erschien, nach 21 Jahren in der 5. Auflage publiziert wird, dann haben die Leser bereits ein klares und positives Urteil über die Qualität des Werkes abgegeben.

In der vorliegenden Neuauflage werden zunächst grundsätzliche dynamische und energetische Probleme sowie die Integration von Teilleistungen besprochen. Es schließen sich Kapitel über Aufnahme und Verteilung von Substanzen sowie über die Regulation des inneren Körpermilieus an. Nach Abhandlung der Aufnahme und Verarbeitung von Informationen behandelt der Autor in einem eigenen Abschnitt die Physiologie der Effektoren, welche das Lebewesen „sinnvoll" auf Informationen aus der Umwelt reagieren lassen. Das letzte Kapitel beschäftigt sich mit der Physiologie des Verhaltens und der Orientierung.

Im Anhang wird eine Zeittafel zur Geschichte der Tierphysiologie, eine Übersicht über das System rezenter Tiere, mehrere Tabellen zu Maßeinheiten, eine Auswahl weiterführender Literatur und ein ausführliches Bildquellenverzeichnis geboten. Ein Register von 27 Seiten und eine Zusammenstellung der benutzten Abkürzungen und Symbole schließen das Werk ab.

Das „Lehrbuch der Tierphysiologie" behandelt die Probleme unter vergleichenden Gesichtspunkten und bezieht sich auf ein breites Spektrum zoologischer Lebensformen. Obwohl viele Einzelbeispiele dargestellt werden, verfällt der Autor nie in „Detailhuberei", sondern arbeitet möglichst die für alle Tiere und den Menschen gleichermaßen gültigen Gesetzmäßigkeiten heraus. Er macht ferner dem Leser bewußt, daß die Anwendung mathematischer, physikalischer und biochemischer Kenntnisse die Darstellung tierphysiologischer Zusammenhänge präzisiert. Die zahlreichen Tabellen und die sorgfältig überarbeiteten Abbildungen erleichtern das Verständnis des im Text vermittelten Stoffes. Der Autor des Lehrbuches vermeidet unzulässige Simplifizierungen und einseitige Darstellungen, er stellt auch widerstreitende Theorien dar.

P. Langer, Gießen

Dyce, K. M.; Sack, W. O.; Wensing, C. J. G.: **Anatomie der Haustiere.** Lehrbuch für Studium und Praxis. Stuttgart: Ferdinand Enke Verlag 1991. 883 S.; zahlr. Abb. DM 248,–. ISBN 3-432-98631-9

An vielen Bildungsstätten hat sich in verschiedenen Ländern seit mehreren Jahren die Problematik ergeben, unter dem Zwang von Studienzeitverkürzungen starke Beschränkungen im fachspezifischen Lehrangebot hinzunehmen, obwohl Wissensumfang und Spezialisierungen beständig stark zunehmen. Diese Tatsache und das Bestreben um internationale Angleichung in der Ausbildungsqualität haben die Veterinäranatomen K. M. Dyce (Edinburgh), W. O. Sack (Ithaca) und C. J. G. Wensing (Utrecht) veranlaßt, eine allgemeine Darstellung über die Anatomie der Haustiere als „Textbook of Veterinary Anatomy" zu verfassen. Diese liegt nun auch in deutscher Sprache vor. Es wurde von den Veterinäranatomen K. D. Budras und K. D. Weyrauch aus Berlin sowie H. Goller, R. R. Hofmann, G. Hummel und Ingrid Goller aus Gießen sachkompetent übersetzt.

Dieses einbändige Lehrbuch ist – dem Untertitel entsprechend – in zwei Teile gegliedert. Im ersten, allgemeinen Teil werden nach einleitenden Darstellungen von Grundfakten und -begriffen Bewegungs-, Verdauungs-, Atmungsapparat sowie Urogenitalsystem, endokrine Drüsen, Herz-Kreislaufsystem, Nervensystem, Sinnesorgane und äußere Haut in einzelnen Kapiteln abgehandelt. Anschauungsobjekt ist der relativ unspezialisierte Hund, aber es werden vielfach zusätzlich die anderen Haussäugetiere vergleichend in Wort und Bild erwähnt. Im wesentlichen wird die Situation beim adulten Tier beschrieben, ontogenetische Lageveränderungen und entwicklungsgeschichtliche Aspekte werden stellenweise zusätzlich angeführt.

Der zweite Teil ist als spezieller Teil stärker den klinischen Anforderungen an den Praktiker gewidmet. Hier wird in 27 Kapiteln die regionale Anatomie des Tierkörpers abgehandelt und spezieller auf Fleischfresser, Pferd, Wiederkäuer und Schwein eingegangen. Ein letztes Kapitel befaßt sich mit der Vogelanatomie.

Das Buch ist verständlich und gut lesbar geschrieben. Nur an wenigen Stellen sind Formulierungen zu bemängeln, weil sie kausale Entwicklungszwänge unterstellen, wie z. B. „Bei Beendigung des Wachstums sind die Schädelnähte nicht mehr notwendig . . ." (S. 66); „Der Wandteil, den die Lippen bilden, hängt von der Ernährungsweise ab, . . .". „Nahrung und Ernährungsweise bestimmen auch die Form der Lippen." (S. 111); „. . . die Nerven, welche die aus den Urwirbeln hervorgehenden Kopfmuskeln versorgen . . ." (S. 343); etc. Dem Text zugeordnet sind sehr viele deutliche und instruktive Schema- und Situationsdarstellungen. Im zweiten Teil fallen besonders mehrere Röntgenaufnahmen auf. Eine gute qualitative Aufmachung rechtfertigt den etwas hohen Preis.

Das Kapitel Nervensystem enthält allerdings einige Schwächen und auch Fehler in wenigen Abb. (z. B. Abb. 8-10; 8-21).

Abgesehen von diesen wenigen Mängeln, die in weiteren Auflagen leicht zu beheben sind, erscheint dieses Buch als eine gelungene Alternative in der Stoffauswahl, die das Anliegen der Autoren erfüllt. Auch der an Anatomie interessierte Säugetierkundler kann es mit Gewinn nutzen.

D. Kruska, Kiel

Corbet, G. B.; Hill, J. E.: **A World List of Mammalian Species.** 3. ed. Natural History Museum Publications. Oxford: Oxford University Press 1991. 243 pp., approx. £ 27.50. ISBN 0-19-854017-5

This treatise is just a list of the scientific names of all mammalian species of the world, their English vernacular equivalents, when available, and their distribution. They are ordered according to Orders, Families and Genera. Some controversies are marked by adding species or generic names in brackets at the appropriate places. References are given for recent changes in nomenclature in addition to some general works. All the remaining complicated accessories of nomenclature and taxonomy (synonym lists, opinions of different authors, author name and year) are omitted. The increase in net number of species from the first (1980) to the second (1986) edition (221) is now smaller with only 93 species in the present book. This is the result of some revisions mainly for Soricidae with 28, Cebidae with 10 and Muridae with 40 more species. Drawings by Ray Burrows give an idea of some of the species listed. A list of 27 extinct species is also now including only mammals that have been known "in the flesh" (e. g. *Thylacinus cynocephalus, Equus quagga,* but also *Pitymys bavaricus* which has not been found again since the description) and a table with species numbers for all Orders in the 6 zoogeographical regions of the world. Much of the decisions in this book are debatable, but the list in general reflects a sober and serious effort and is also informative concerning the consequences of recent taxonomic work. It is a good balance between flexibility due to scientific progress and stability necessary for practical work.

J. Niethammer, Bonn

Kurt, F.: **Das Reh in der Kulturlandschaft.** Sozialverhalten und Ökologie eines Anpassers. Hamburg und Berlin: Paul Parey 1991. 284 S., 126 Abb., 18 Tab. Geb. DM 68,–. ISBN 3-490-17618-9

In dieser Abhandlung hat der Autor, ein ausgewiesener Rehforscher, die Fülle der wissenschaftlichen Literatur über das Reh, fußend auf seinen eigenen Untersuchungen und den umfangreichen Studien von Strandgaard (1972) und Ellenberg (1978), zusammenfassend erarbeitet.

Wesentliche Zielsetzungen sind dem Titel zu entnehmen: Es geht um die Lebensbedingungen und Lebensmöglichkeiten des Rehs in der Kulturlandschaft, also in der vom Menschen beeinflußten, ja gestalteten Landschaft. Eine Kulturlandschaft kann reich strukturiert sein durch Wechsel von artenreichem, durch Lichtungen unterbrochenem Wald mit kleinräumigen Feldern und Wiesenarealen, die durch Wallhecken begrenzt sind. Sie kann aber auch aus eintönigen Monokulturen bestehen, seien es ‚Holzplantagen' oder eintönige Agrargebiete. Entsprechend solchen verschiedenen Gegebenheiten zeigt das Reh Unterschiede im Sozialverhalten und in seinen Wechselbeziehungen mit seiner Umwelt. So unterscheiden sich Waldrehe und Feldrehe beträchtlich voneinander: Während z. B. Weibchensippen und Ein-Mann-Familien in waldreichen Gebieten zu beobachten sind, kommt es beim Feldreh zur Rudelbildung. Diesem unterschiedlichen Sozialverhalten entsprechend ist beim Feldreh im Unterschied zum Waldreh keine Territorialität zu beobachten.

Anpassungen an eine offene Landschaft sind besonders für die moderne Kulturlandschaft typisch, in der zudem natürliche Beutegreifer fehlen. So kann es zu beträchtlichen Bestandszunahmen kommen. Wenn dann nach der Erntezeit das offene Land nicht mehr genügend Nahrung bietet, wandern die Rehe in großer Zahl in den Wald; dort verursachen sie erhebliche Verbißschäden. Vielmehr als zu geringe Jagd sind es also Veränderungen der natürlichen Umwelt, denen sich das Reh anzupassen weiß, die letztendlich zu Waldschäden führen. Kurt plädiert dafür, das Rehwild auf eine Bestandsgröße zu regulieren, bei der die Artenvielfalt der Lebensgemeinschaft Wald ebensowenig gefährdet wird wie dessen natürliche Verjüngung. Das ist aber nur möglich, wenn man über das Reh und seine sozialen und ökologischen Bedürfnisse sowie über seine vielfältigen Anpassungsmöglichkeiten Bescheid weiß.

Diese Kenntnisse vermittelt das Buch in umfassender Weise. Es ist in zehn Themen gegliedert: Das 1. Kapitel referiert Stand und Probleme der Rehwildforschung. Das 2. Kapitel vermittelt dem Leser die wesentlichen ökologischen Ansprüche des Rehs. Die Kapitel 3–8 behandeln die verschiedenen Aspekte des Sozialverhaltens in seiner Abhängigkeit von ökologischen Gegebenheiten. In den letzten beiden Abschnitten erläutert der Autor die Bestandszunahmen und die heutige Bestandssituation sowie daraus abzuleitende Erfordernisse für die Bejagung.

Das Buch ist sehr anschaulich geschrieben und mit zahlreichen Tabellen und Abbildungen ausgestattet, die der Rezensent allerdings zum Teil als schwer lesbar empfindet. Da der Leserkreis

wohl nicht allein auf Jäger beschränkt sein soll, wäre ein gesondertes Glossar der zahlreichen jagdlichen Ausdrücke wünschenswert gewesen. Ärgerlich ist, daß mehrere zitierte Arbeiten unter der Literatur nicht verzeichnet sind, z. B. HOFMANN 1979 (S. 262), MAGGIO 1988 (S. 261), MEUNIER 1979 (S. 243) und noch weitere. Diese Mängel schmälern allerdings nicht den Gesamteindruck: ein sehr empfehlenswertes Buch. D. HEINRICH, Kiel

RÜSSE, I.; SINOWATZ, F.: **Lehrbuch der Embryologie der Haustiere.** Berlin, Hamburg: Paul Parey 1991. 473 S.; 318 Abb.; 39 Tab. DM 178,–. ISBN 3-489-57716-7

Dieses Lehrbuch der Münchener Veterinäranatomen ist in neuer und modernisierter Fassung als Nachfolgewerk der Entwicklungsgeschichte der Haustiere von ZIETZSCHMANN und KRÖLLING konzipiert, vornehmlich für Studierende der Veterinärmedizin, aber auch Humanmedizinern und Biologen anempfohlen. Der Stoff wird in mehreren Abschnitten in einem allgemeinen und einem speziellen Teil geboten, vorangestellt ist eine Geschichte der Embryologie der Haustiere von A. VON DEN DRIESCH. Die beiden Autoren teilen sich die Aufgabe, indem sie für die verschiedenen Abschnitte entweder einzeln oder gemeinsam verantwortlich zeichnen. Im allgemeinen Teil werden behandelt: Prinzipien der Entwicklung und Morphogenese; Gametogenese; weiblicher Sexualzyklus; Befruchtung und Teilung; Gastrulation; Keimblattbildung und Bildung der Körpergrundgestalt; Frühgravidität, Implantation und Plazentation. Der spezielle Teil befaßt sich mit Herz- und Kreislaufsystem; Nervensystem; Sinnesorganen; Harn- und Geschlechtsorganen; Verdauungskanal und Anhangsorganen; Atmungsorgan; Körperhöhlen; Bewegungsapparat; Haut- und Anhangsorganen; Gesicht und Körperform; Mißbildungen. In mehreren Abschnitten stehen die Haustiere Rind, Schaf, Schwein, Pferd, Hund, Katze, Huhn im Vordergrund, andere Kapitel enthalten allgemeinere Beschreibungen. Das Buch ist mit zahlreichen Abbildungen von Präparaten sowie Skizzen und Übersichtszeichnungen eindrucksvoll illustriert. Viele Tabellen kennzeichnen darüber hinaus artspezifische Entwicklungsstadien in zeitlicher Zuordnung.

Der Text liefert grundsätzlich viel Information, vor allem einige neuere Erkenntnisse im Detail. Allerdings machen sich mehrere Schwächen bemerkbar, vor allem aus zoologischer Sicht, weil der evolutive Wandel der Ontogenesen im Tierreich nur sporadisch angedeutet bleibt. Die verschiedenen Abschnitte sind inhaltlich unterschiedlich weit gefaßt und wenig konsequent begrenzt. Die Darstellung der Gametogenese ist z. B. sehr ausführlich, bleibt aber auf placentale Säugetiere und auf Vögel beschränkt. Im Kapitel über Gastrulation hingegen wird zusätzlich sogar auf Branchiostoma, Seeigel und Amphibien eingegangen. Der spezielle Teil behandelt fast ausschließlich die Organsysteme der Säugetiere in der Embryogenese, auf den Vertebraten Vogel wird kaum eingegangen. Zusätzlich sind die sprachlichen Formulierungen an vielen Stellen ungenau, verwirrend oder mißverständlich, aber auch komplizierend. Folgende Beispiele mögen das belegen: die Eizelle hat einen „Cortex"; „die Eizelle ist der Dotter"; „die Spermien wandern um die Ovulation den Eileiter hinauf"; einmal ist von Replikation, dann wiederum von Reduplikation die Rede; „die Blastocyste enthält ein Blastocoel"; „das Ei entwickelt sich an der Oberfläche des Dotters"; „das zephale Ende des Primitivstreifens"; Somite sind „Urwirbel"; „die Erkennung der Gravidität seitens des Muttertieres..."; „zwischen Amnion und Chorion ist die seroamniotische Platte"; „die Vorniere ist in der Tierreihe bis zu dem primitiven Fischen funktionstüchtig"; etc. Störend sind ferner häufige Wiederholungen vorher geschilderter Sachverhalte und neu eingeführte lateinisch-griechische Mischprodukte in der Fachsprache, denn es gibt nun Ovogenese, Ovogonie und Ovozyten, aber immer noch einen Cumulus oophorus. Auch stimmen die Abbildungen nicht immer mit den Ausführungen in Legenden und Text überein.

Insgesamt liegt damit eine recht heterogene Darstellung vor, die dem Studenten als Lehrbuch den Zugang zum ohnehin komplexen und komplizierten Wissensstoff wenig erleichtert. D. KRUSKA, Kiel

KOLB, GERTRUD M. H.: **Vergleichende Histologie, Cytologie und Mikroanatomie der Tiere.** Berlin, Heidelberg, New York: Springer-Verlag 1991. 352 pp., 201 Abb., 2 Farbtaf. brosch. DM 48,–. ISBN 3-540-52842-3

Von der Autorin wird ein ‚Springer-Lehrbuch' der vergleichenden Histologie der Tiere unter Berücksichtigung der Cytologie und mikroskopischen Anatomie geboten, welches „für Studenten der Biologie, Veterinärmedizin und für naturwissenschaftlich Interessierte" gedacht ist. Dabei wird bewußt auf die Darstellung spezieller Details verzichtet. Die Mehrzahl der Abbildungen ist der Literatur entnommen. Wirbeltiere sind in diesem Buch ausführlicher dargestellt als Wirbellose.

Nach einer kurzen Übersichtsdarstellung der mikroskopischen Technik werden in fünf Kapiteln die Gewebetypen dargestellt: Epithelien, Drüsen, Binde- und Stützgewebe, Blut und freie Zellen des Bindegewebes, Muskelgewebe. Anschließend werden unter Berücksichtigung funktionell-anatomischer Gesichtspunkte in sieben Kapiteln Organe im Systemzusammenhang besprochen: Aufnahme und Weiterleitung von Information, Integument, Zahn- und Zahnentwicklung, Zunge, Transport-,

Speicher- und Resorptionssysteme, Systeme des Stoffaustausches und Permeabilität, Fortpflanzungsorgane.

Die Gewichtung der besprochenen Systeme ist auffällig ungleichmäßig. So ist beispielsweise der Zunge von Amphibien und Säugetieren und sehr knappen Hinweisen auf die Verhältnisse bei anderen Wirbeltiergruppen ein kurzes eignes Kapitel gewidmet, welches typographisch gleichartig dargestellt wird wie das ausführlichere Kapitel über die Systeme der Aufnahme und Weiterleitung von Information, dessen Anfangsabschnitt zunächst eine allgemeine Darstellung der Nervengewebe sowie der Synapsen und der Glia bietet. Eine anschließende Übersicht stellt jeweils in wenigen Zeilen Nervensysteme im Tierreich für Taxa, wie beispielsweise Cnidaria, Plathelminthes, Echinodermata oder Polychaeta, dar. Das Nervensystem der Wirbeltiere wird auf anderthalb Seiten abgehandelt.

Die Veröffentlichung macht dem Leser bewußt, daß das Tierreich auch heute noch außerordentlich ungleichmäßig intensiv mikroskopisch-anatomisch studiert worden ist. Entsprechend interessierte Zoologen sollten in diesem Buch einen Ansporn zu Untersuchungen bisher wenig berücksichtigter Bereiche der vergleichenden Histologie sehen. Insbesondere bei den Wirbellosen und den Nonmammalia unter den Wirbeltieren bietet sich ein weites Feld möglicher Untersuchungen.

P. LANGER, Gießen

STEPHAN, H.; BARON, G.; FRAHM, H. D.: **Comparative Brain Research in Mammals.** Vol. 1: Insectivora. Berlin, Heidelberg, New York, London: Springer-Verlag 1991. 573 pp., figs. and tables. DM 146,–. ISBN 3-540-97505-5

Over a period of 40 years HEINZ STEPHAN from the Max-Planck-Institut für Hirnforschung, Frankfurt/M. has studied comparative brain anatomy in many mammals. During this time he initiated appropriate research both nationally and internationally. This volume is the first in a survey series, where he together with GEORG BARON (Montreal) and HEIKO D. FRAHM (now Köln) characterizes the brains of insectivores covering the whole of their diversification. Further volumes, dealing with the brains of Chiroptera, marsupials, and primates are still in progress.

This book is presented in several chapters. Following short introductory remarks, a compilation of investigated species and a list of abbreviations are presented. The material and methods chapter clearly describes: fixation and preparation of brains, determination of fresh brain weights, a compilation of brain and body weights, comparison of linear brain measurements, brain sectioning, determination of volumes, evaluation of species-specific standards, survey of structures and complexes, variability, and methods of comparing brain size and volume. Especially under the last heading the interspecific allometric method of comparing fresh tissue size based on a brain-to-body weight relation is explained and reviewed critically.

In the following chapter comparative aspects of brain characteristics are highlighted, and data are documented on an unusually large spectrum of species and number of specimens worldwide in their distribution. Here, the external appearance of the brains of insectivores is described qualitatively, and several parts and components of the brain are characterized with respect to their histology, configuration and size. According to calculations of indices clear differences exist in the total brain sizes of the species investigated independent of a body size influence and thus, all the other structures measured vary in absolute and relative size. The sub-family Geogalinae with the single representative *Geogale aurita* from Madagaskar shows by far the most primitive brain characteristics and the smallest brain size. Furthermore, indices calculated for average levels of brain sizes within sub-families result in the following arrangement from small to large brain size: Tenrecinae, Erinaceinae, Crocidurinae, Soricinae, Oryzorictinae, Potomogalinae, Chrysochlorinae, Talpinae, Solenodontinae (*Solenodon paradoxus*), Echinosoricinae, Desmaninae. The same has been calculated for the classical parts of the brain and certain other components. For the first time data on 20 nuclei of the medulla oblongata are presented as well as data on several nuclei and structures of the mesencephalon, the cerebellum, the diencephalon and the telencephalon. A size comparison of some main brain complexes with those of primates (prosimians, non-human simians, *Homo*) is additionally included.

The next chapter is devoted to the brain characteristics of the taxonomic units, thus resulting in a highly diverse and heterogeneous brain composition of the extant species within this order.

These differences are discussed in the following two chapters in connection with phylogenetic and evolutionary adaptive radiation in general and with ecoethological adaptations in particular (surface dwellers, fossorial species, semi-aquatic species, winter survival).

The final chapter is devoted to brain characteristics related to functional systems, e.g., olfactory (main and accessory), visual, somatosensory, auditory, vestibular, motor, limbic and the neocortex. There are 50 pages of references, 74 tables added in the appendix and a very impressive and detailed stereotaxic atlas of the brain of *Atelerix algirus* cut in the frontal plane. 108 figures and further tables are distributed throughout the text.

This book is well written, and the most accurate analysis and documentation on the topic presented to date. It is a valuable resource book, not only of interest to neuroanatomists but also to mammalogists in general, due to its high biological significance.

D. KRUSKA, Kiel

Deutsche Gesellschaft für Säugetierkunde: Referate, Vorträge und Posterdemonstrationen der 65. Hauptversammlung 1991

Ein Hauptziel der Deutschen Gesellschaft für Säugetierkunde ist, auf ihren Jahrestagungen über Säugetiere arbeitende Wissenschaftler verschiedenster Fachrichtungen zusammenzuführen, den Gedanken- und Erfahrungsaustausch anzuregen, um so Erkenntnisse aus den einzelnen Forschungsgebieten zu integrieren. Schwerpunkte der diesjährigen Tagung der Deutschen Gesellschaft für Säugetierkunde sind die Themenbereiche »Systematik und Stammesgeschichte der Säuger«, »Anpassung an aquatische Lebensräume« und »Domestikation«. Das vorliegende Sonderheft zum Band 56 der »Zeitschrift für Säugetierkunde« enthält demgemäß die Kurzfassungen von Vorträgen zu diesen Schwerpunkten und, einer Tradition der Gesellschaft folgend, zu andersartigen Themen sowie zu den während der Tagung gezeigten Postern. Alle Kurzfassungen sind zusammen nach Autorennamen in alphabetischer Reihenfolge geordnet. 67 angemeldete Vorträge, Filmdarbietungen und Posterdemonstrationen weisen auf die wissenschaftliche Breite der Gesellschaft hin und lassen auf einen interessanten, regen Gedankenaustausch hoffen. Die Deutsche Gesellschaft für Säugetierkunde tagte erstmalig seit 30 Jahren wieder in Hamburg. Die Kurzfassungen der Vorträge und Posterdemonstrationen der Deutschen Gesellschaft für Säugetierkunde sind ab der 58. Hauptversammlung 1984 in Göttingen noch lieferbar. Zu beziehen durch jede Buchhandlung. ★ **Deutsche Gesellschaft für Säugetierkunde. 65. Hauptversammlung in Hamburg, 22. bis 26. September 1991.** Kurzfassungen der Vorträge und Posterdemonstrationen. Herausgegeben von Dr. Christel Schmidt, Bonn, und Prof. Dr. Harald Schliemann, Hamburg. 1991. 53 Seiten. Kartoniert 24,– DM

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Erscheinungsweise und Bezugspreis 1992: 6 Hefte bilden einen Band. Jahresabonnement Inland: 358,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 371,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 358,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 57 (1992) 4, 193–256

Boar Semen Preservation II

Proceedings of the Second International Conference on Boar Semen Preservation, held at Beltsville, August 1990

Edited by Prof. Dr. L. A. Johnson, Beltsville Agricultural Research Center, USA and Dr. D. Rath, Institut für Tierzucht und Tierverhalten Mariensee, Bundesforschungsanstalt für Landwirtschaft Neustadt.

Dedicated to the memory of Kjell Larsson.

Supplements to Reproduction in Domestic Animals, No. 1

1991. 424 pages with 73 figures and 97 tables. Soft cover DM 58,–
ISBN 3-489-53316-X

These proceedings are the compilation of papers presented at the Second International Conference on boar semen preservation held at Beltsville, Maryland, USA. The Conference, the Second in the series was devoted to the subjects of deep frozen and liquid stored boar semen. Twenty-one papers were presented by outstanding scientists. Areas covered were: The epididymis, testis and sperm maturation; fundamental cryobiology; an update on the state of the art relative to frozen boar semen; semen evaluation; liquid semen production, preservation and use; management of semen production and artificial insemination and new technologies in swine reproduction. In addition there are updates on the commercial use of swine artificial insemination from 11 different countries of the world. Short papers or abstracts are also included from the 33 posters presented at the Conference.
Boar Semen Preservation II is mandatory reading for anyone interested in Animal Reproduction or the overall field of Animal Science. The book will be essential to those interested in sperm preservation and storage at the basic and the applied level.



Berlin and Hamburg

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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

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Preliminary observations on the comparative gastric morphology of selected Old World and New World bats

By M. R. Perrin and J. J. Hughes

Department of Zoology and Entomology, University of Natal, Pietermaritzburg, R.S.A.

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Abstract

Stomachs of ten species of bats (eight microchiropteran and two megachiropteran species), representing nine genera from five families, were examined and compared morphologically and histologically. All stomachs were wholly glandular but differences in gross morphology were observed between insectivorous, omnivorous and frugivorous species. Anatomical variatons in the gastric mucosa between species were minor. The insectivorous bats exhibited little variation between species and possessed a simple tubular gastric stomach. The stomachs of the frugivorous species were more specialised with increased compartmentalisation. Scanning electron microscopy revealed the presence of microvilli in the stomachs of both an insectivorous and a frugivorous species.

Introduction

The gastrointestinal morphology of bats approximates that of other mammals in general organisation (Hill and Smith 1984). Most mammals have a single chambered (unilocular) stomach although ruminants and other foregut fermenters possess a multichambered (plurilocular) stomach which is an adaptation to herbivory (Madge 1975). Feeding styles found among bats include insectivory, piscivory, omnivory, nectarivory, frugivory and sanguinivory, and these are reflected in the anatomy of various regions of the digestive tract.

The gross morphology and ultrastructure of the stomach of many microchiropteran species have been reported (Kamiya and Pirlot 1975; Forman 1972; Rouk and Glass 1970), but little attention has been devoted to the digestive tract of the Megachiroptera (Okon 1977; Bhide 1980; Tedman and Hall 1985a, b). The stomachs of *Epomophorus wahlbergi* and *Eonycteris spelaea* as in *Eidolon helvum* (Okon 1977), *Rousettus leschenaulti* (Bhide 1980), and *Pteropus alecto* and *P. poliocephalus* (Tedman and Hall 1985a, b) are large and saccular with an expanded cardiac and fundic region and a well developed pyloric tube. The pyloric sphincter is asymmetrical. These features are also characteristic of frugivorous microchiropteran species and serve to increase surface area for digestion.

Kamiya and Pirlot (1975) interpreted stomach structure as plesiomorphic in insectivorous bats, transitional in nectar feeders and apomorphic in frugivorous, and especially sanguinivorous, bats. They noted only minor differences in gastric anatomy between Old World and New World insectivorous species and also suggest that the Old World (frugivorous) pteropodids are more specialised for a vegetarian diet than the New World phyllostomatids. It is suggested that the pteropodids followed an independent path of evolution towards vegetarianism before that of the phyllostomatids, and that similarities between the two families are likely a result of convergence (Stephan and Pirlot 1975; Kamiya and Pirlot 1975).

Gastric histology and histochemistry have been used to reveal systematic relationships of bats (Forman 1972; Kamiya and Pirlot 1975), particularly in the Phyllostomatidae.

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This examination was undertaken to determine whether gross gastric anatomy can be correlated with feeding specialisations (Carleton 1973; Perrin and Curtis 1979) and phylogeny (Perrin and Curtis 1979).

Material and methods

The African species were euthanised with carbon dioxide. Stomachs used for histological and morphological studies were fixed in Bouin's fixative for 18 h after which they were stored in 70 % alcohol. The stomachs of the non-African species, which had been stored in 10 % formalin for up to three years, were also placed in 70 % alcohol. Gross morphology was first examined by bisecting the stomach sagittally. Stomachs less than 1 cm in length were photographed with an Olympus B/H2 photomicroscope and larger stomachs with a Pentax SP II camera fitted with a Pentax macro lens. They were than placed into one of the categories defined by Forman (1972). These include: a. "regular", b. "funnelled", and c. "elongated". The authors recognise a further two forms, "recurved" and "tubular" (Table).

Stomachs for histology were embedded in paraffin wax, sectioned at 6–9 μ, and stained with Ehrlich's haematoxylin and eosin, Periodic Acid Schiff (PAS) (Humason 1967), or Ayoub and Shklar (1983). Light micrographs were taken through a Leitz Laborlux 12 microscope equipped with a Wild Photoautomat MPS 45/51 camera.

For scanning electron microscopy (SEM) small pieces (3 × 3 mm) of stomach tissue were fixed in 3 % cold buffered glutaraldehyde for a minimum of 12 h. The tissue was subsequently critical point dried, coated with gold palladium and viewed with a Hitachi S-570 scanning electron microscope (Cross 1979).

Results

The terminology used in describing the anatomical form of a hypothetical "generalised" chiropteran stomach is presented in Figure 1.

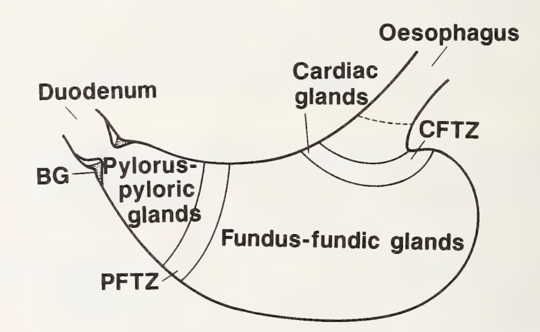


Fig. 1. A diagram to represent a generalised chiropteran stomach. BG = Brunner's glands, CFTZ = cardiofundic transition zone, PFTZ = pyloric-fundic transition zone

Gross morphology

Insectivorous species

The stomachs of the African insectivorous bats, *M. schreibersi, M. fraterculus, R. simulator* and *M. tricolor* are categorised as "regular" and exhibit the simplified tubular gastric form (Fig. 2). They are reniform and generally symmetrical with the greater and lesser curvature nearly parallel. The stomachs are relatively short and the terminal portion (distal to the gastro-oesophageal junction) is equal in length to that of the fornix ventricularis. In *M. tricolor,* however, the fundus is elongated (Fig. 3). The pyloric sphincters of all these species are symmetrical.

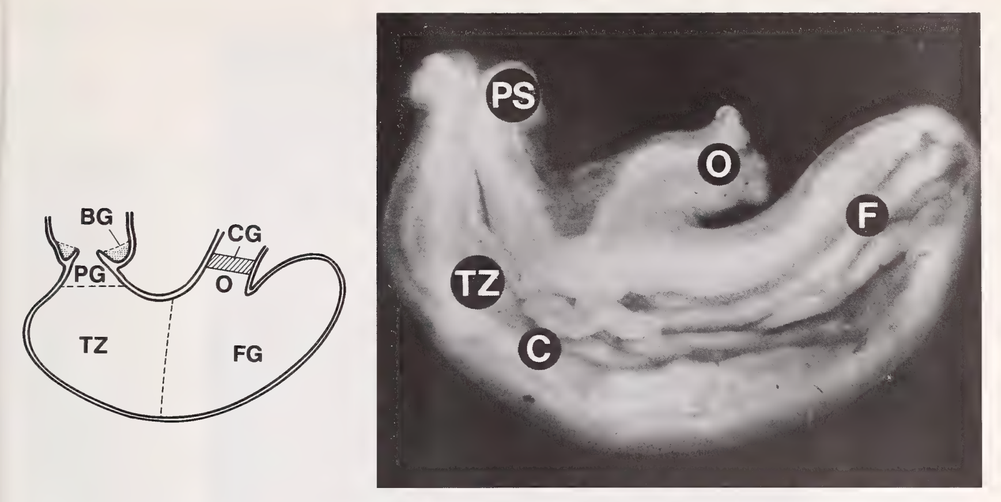


Fig. 2 (left). Diagrammatic representation of a 'regular' chiropteran stomach. BG = Brunner's glands, CG = cardiac glands, FG = fundic glands, PG = pyloric glands, TZ = transition zone. (*Miniopterus schreibersi* × 5,6). – *Fig. 3 (right).* The bisected stomach of *Myotis tricolor* showing the sharply angled oesophagus and elongated fundus. C = corpus, F = fundus, O = oesophagus, PS = pyloric sphincter, TZ = transition zone

Omnivorous species

In the "elongated" stomach of *P. hastatus* the cardiac vestibule is reduced to a vestige (Fig. 4) while in *G. soricina* it is absent (Fig. 5). The fornix ventricularis is dilated and expanded dorsally in both species. The terminal tubular stomach is extensive in *G. soricina*

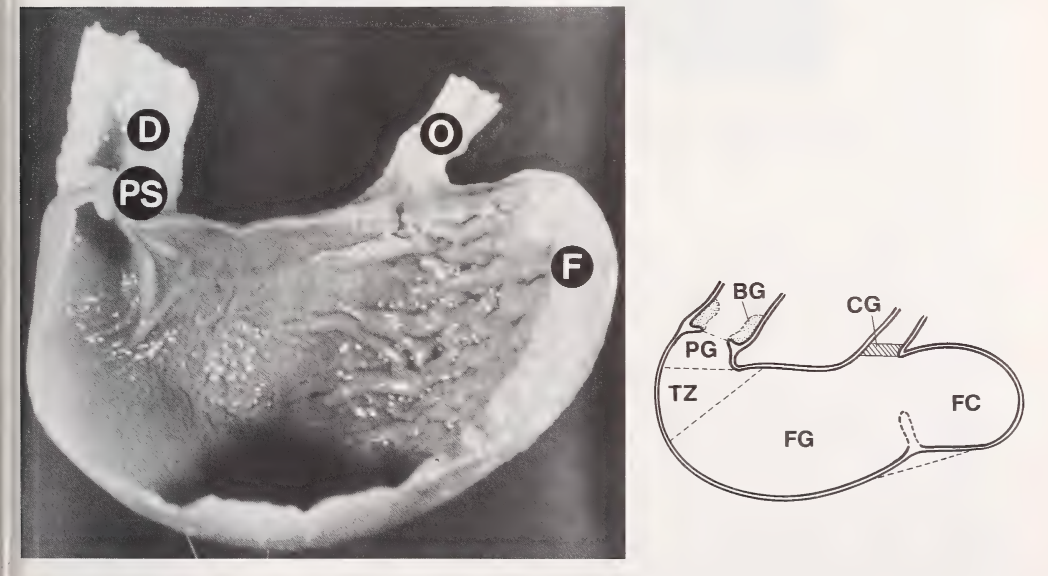


Fig. 4 (left). The bisected stomach of *Phyllostomus hastatus.* D = duodenum, F = fundus, O = oesophagus, PS = pyloric sphincter. – *Fig. 5 (right).* Diagrammatic representation of an 'elongated' chiropteran stomach. BG = Brunner's glands, CG = cardiac glands, FC = fundic caecum, FG = fundic glands, PG = pyloric glands, TZ = transition zone (*Glossophaga soricina* × 6,3)

and *P. hastatus*, and the pyloric sphincters are asymmetrical (since the valves are larger on the greater than the lesser curvature).

Nectarivorous species

Eonycteris spelaea has a markedly sacculated stomach which is extensively elongated, forming a tubular structure (Fig. 6). It is specialised and is here defined as "tubular". The large fornix ventricularis is separated from the fundus by a fold of the stomach wall. The cardiac vestibule is narrow while the fundus forms the elongated tubular portion of the stomach.

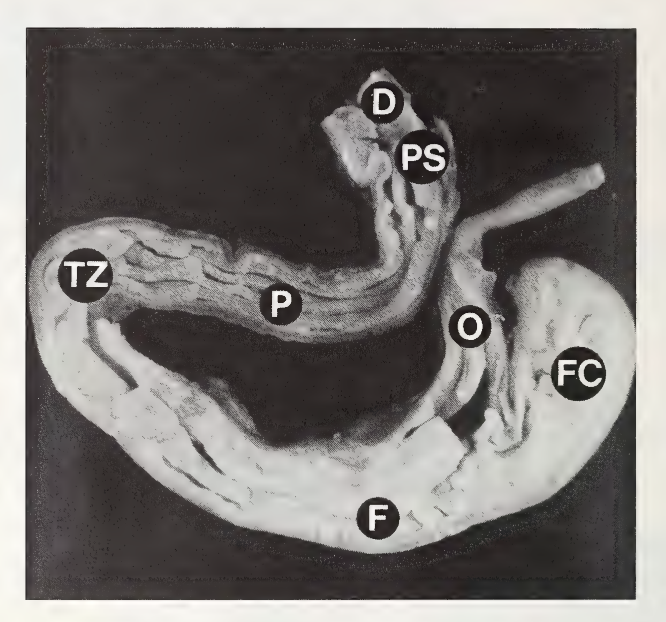


Fig. 6. The bisected stomach of *Eonycteris spelaea.* D = duodenum, F = fundus, FC = fundic caecum, O = oesophagus, P = pylorus, PS = pyloric sphincter, TZ = transition zone

Frugivorous species

Artibeus sp. has a saccular stomach with an unusually large fornix ventricularis and a long broad cardiac vestibule (Fig. 7). The pyloric tube is relatively long and narrow and has a pronounced sulcus intermedius. *Artibeus* exemplifies the "funnelled" stomach condition (Fig. 8).

The stomach of *B. cavernarum* is tubular and reniform and the terminal fundic area is large and recurved (Fig. 9). It is here defined as the "recurved" stomach type. The fundic caecum is also recurved and elongate while the oesophagus enters the stomach at a slight angle. There is a pronounced pyloric constriction and the pyloric sphincter is symmetrical.

E. wahlbergi has a modified 'recurved' saccular stomach with an elongated, recurved fundic caecum (Fig. 10). The fundus, corpus, pyloric antrum and pyloric canal are demarcated externally by constrictions in the stomach wall. The pyloric canal is elongated and the pyloric sphincter is symmetrical.

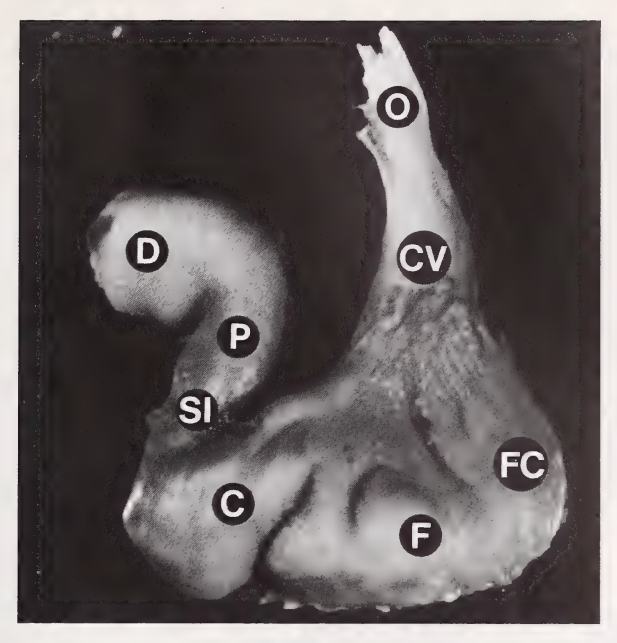


Fig. 7. External view of the whole stomach of *Artibeus* sp. C = corpus, CV = cardia vestibule, D = duodenum, F = fundus, FC = fundic caecum, O = oesophagus, P = pylorus, SI = sulcus intermedius

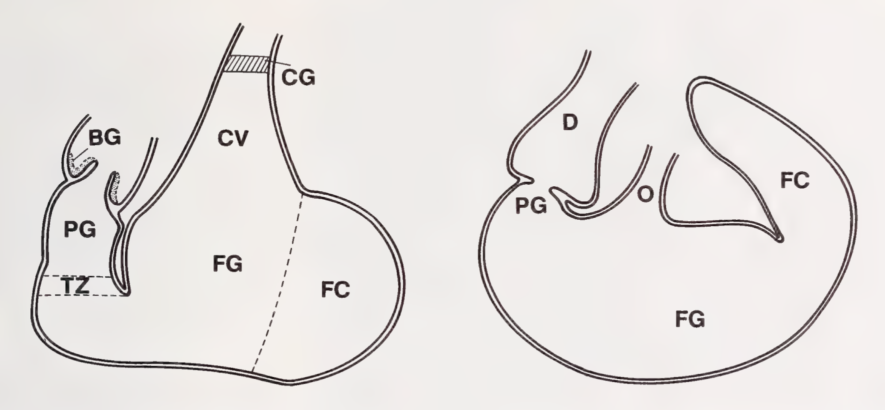


Fig. 8 (left). Diagrammatic representation of a 'funnelled' chiropteran stomach. BG = Brunner's glands, CG = cardiac glands, CV = cardiac vestibule, FC = fundic caecum, FG = fundic glands, PG = pyloric glands, TZ = transition zone. (*Artibeusf* sp. × 6,3). – *Fig. 9 (right).* Diagrammatic representation of the 'recurved' stomach condition. FG = fundic glands, PG = pyloric glands, FC = fundic caecum, D = duodenum, (*Brachyphylla cavernarum* × 3,8)

Musculature

The muscularis externa of the insectivorous bats is exceptionally thick throughout the stomach (Fig. 3), and is approximately twice as thick as that of the frugivorous *E. wahlbergi.* In *E. wahlbergi* (Fig. 10), only the circular muscle throughout the greater curvature of the pyloric tube appears to be particularly thickened.

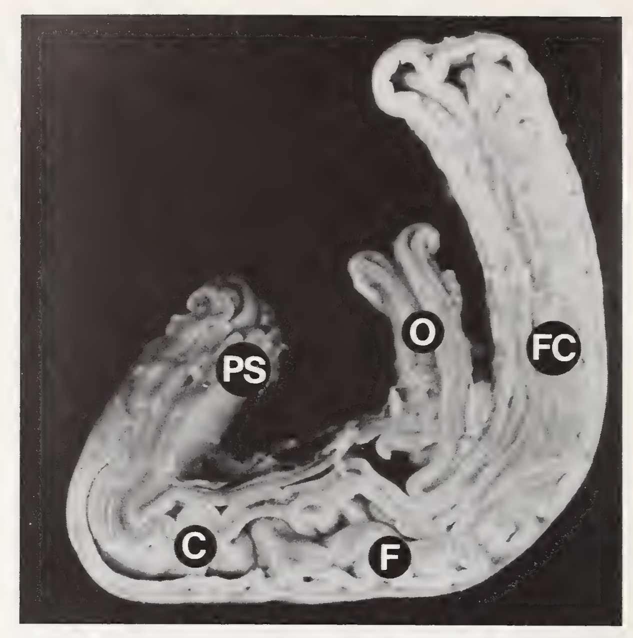


Fig. 10. The bisected stomach of *Epomophorus wahlbergi* (× 3). F = fundus, FC = fundic caecum, O = oesophagus, PS = pyloric sphincter, C = corpus

Pyloric sphincter

The pyloric sphincters of each African insectivorous species examined are symmetrical, and typically possess thick muscle layers. The omnivorous species, *P. hastatus* and *G. soricina*, however, have long asymmetrical valves which are longer on the greater curvature (Figs 4, 5).

In the nectarivore, *E. spelaea,* the musculature is evenly developed on both sides of the pyloric valve. A well-developed valve on the greater curvature is present in *B. cavernarum.* In contrast to the other frugivorous bats, the pyloric sphincter in *E. wahlbergi* is asymmetrical. The musculature is thicker in the valve on the lesser curvature, while the valve on the greater curvature is longer and thinner.

Gastric mucosa

The stomachs of all the species examined are wholly glandular. Fundic glands occupy most of the mucosal surface area, and these are characterised by their long slender appearance, and the presence of chief and parietal cells within the gland (Fig. 11). Under SEM the pyloric and fundic regions are characterised by deep infoldings, the gastric pits. The glands open into these recesses and the columnar epithelial cells show a typical "cobblestone" surface appearance (Fig. 12).

Microvilli are present in the stomach of *M. schreibersi* and are short and sparsely distributed. However, scanning electron microscopy reveals the presence of numerous elongate microvilli throughout the stomach of *E. wahlbergi* (Fig. 13). Yeast and fungal spores (possibly *Penicillium* or *Argostium*) are particularly abundant in the megachiropteran fruit bat, *E. wahlbergi* (Fig. 14), but are also common in the African insectivorous bat species. No bacteria or other symbiotic organisms were observed in any of the bat stomachs examined.

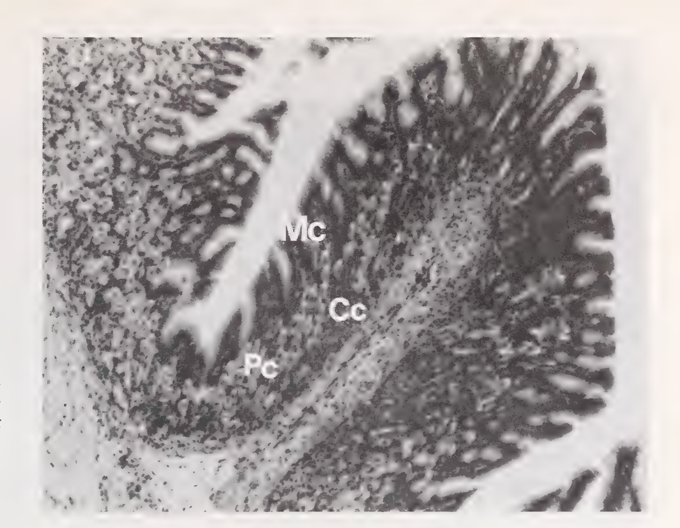


Fig. 11. The fundic glands in the corpus of *Epomorphus wahlbergi* (× 550). Cc = chief cells, GP = gastric pit, Mc = mucoid cells, Pc = parietal cells

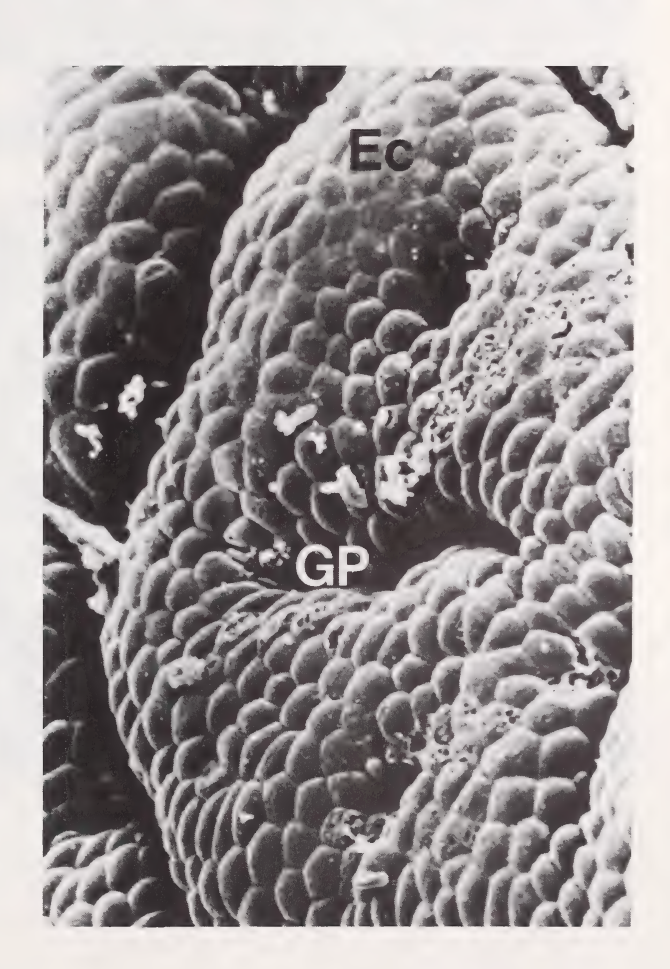


Fig. 12. A scanning electron micrograph of the "cobblestone" surface of the fundic glands in *Miniopterus schreibersi* (× 480). Ec = epithelial cells, GP = gastric pit

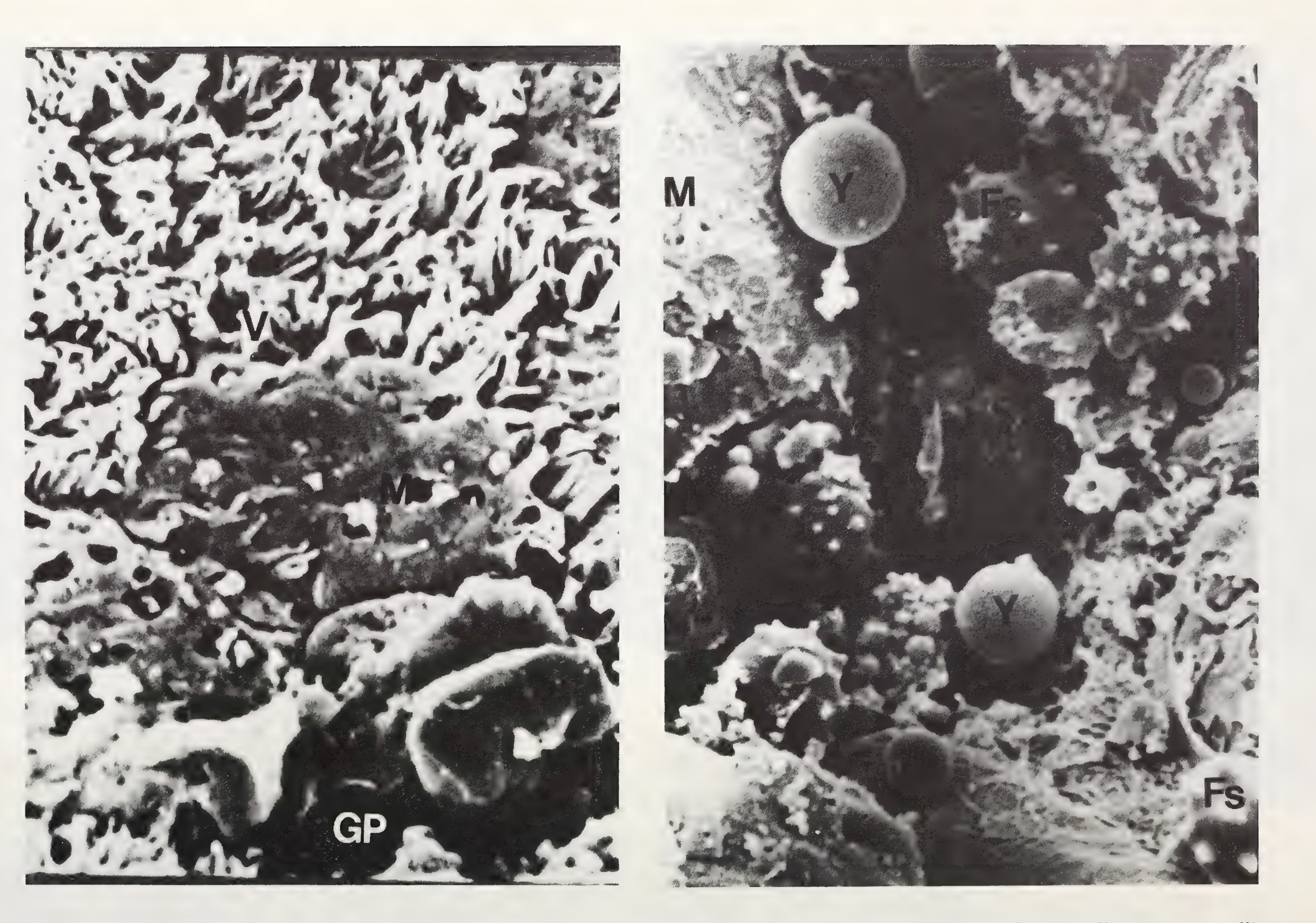


Fig. 13 (left). Scanning electron micrograph of the fundus of *E. wahlbergi*, showing the numerous elongated microvilli. V = microvilli, M = mucus, GP = gastric pit. – *Fig. 14 (right).* Yeast and fungal spores in the stomach of *Epomophorus wahlbergi* (× 3400). FS = fungal spores, M = mucus, Y = yeast cell

Discussion

Gross morphology

Variation in gross gastric morphology is extensive among the bat species examined, but similar trends exist among closely-related genera and among bat species with similar food habits. Several broad categories of gastric anatomy are recognised, named and exemplified. These include regular (*M. schreibersi*), funnelled (*Artibeus* sp.), elongated (*P. hastatus*), recurved (*B. cavernarum*) and tubular (*E. spelaea*).

Characteristics of the bat stomachs studied

Species	Stomach type	Dietary guild	Family
Rhinolophus simulator	Regular	Insectivorous	Rhinolophidae
Myotis tricolor	Regular	Insectivorous	Vespertilionidae
Miniopterus schreibersi	Regular	Insectivorous	Vespertilionidae
Miniopterus fraterculus	Regular	Insectivorous	Vespertilionidae
Epomophorus wahlbergi	Recurved	Frugivorous	Pteropidae
Artibeus sp.	Funnelled	Frugivorous	Phyllostomatidae
Brachyphylla cavernarum	Recurved	Frugivorous	Phyllostomatidae
Phyllostomus hastatus	Elongated	Omnivorous	Phyllostomatidae
Glossophaga soricina	Elongated	Omnivorous	Phyllostomatidae
Econycteris spelaea	Tubular	Nectarivorous	Pteropidae

The funnelled and elongated stomachs have well developed, or reduced/absent, cardiac vestibules respectively, but each has a large fornix ventricularis. The former characterises frugivores while the latter exemplifies a condition intermediate between herbivores and carnivores.

Forman (1972) suggests that the sharply-angled pyloric tube of the recurved stomach has a distinctive crook at the point of recurvature, when the stomach is distended. This might serve to retard the rapid transport of food through the stomach and cause foods that are difficult to digest, to be exposed longer to digestive enzymes.

The tubular stomach of *E. spelaea* resembles that of *Artibeus* with respect to the cardiac vestibule and fornix ventricularis. In pteropodids, the cardiac vestibule is more evident than in phyllostomatids (Kamiya and Pirlot 1975), while the angled pyloric segment of the pteropodids is as marked as that observed in *Artibeus* sp. Similarities also exist between *E. spelaea* and *Rousettus leschenaulti* (Bhide 1980), since the stomachs become progressively narrower from the fornix ventricularis to the pyloric region, and the tubular portions reflex sharply.

Musculature

At the gastro-oesophageal junction in *E. wahlbergi*, there is a sphincter-like development of the muscularis externa. This resembles similar structures in *E. helvum* (Okon 1977), *P. alecto* and *P. poliocephalus* (Tedman and Hall 1985a, b). It is, however, absent in *R. leschenaulti* (Bhide 1980). The sphincter may be important in resisting back pressure from liquid food material contained within the stomach, especially when hanging upside down.

The insectivorous bats reveal a much greater degree of muscular hypertrophy throughout the stomach than the frugivorous species. The prominent musculature of the insectivorous bats is of great advantage in increasing the area over which large rhythmical contractions can take place, thereby assisting gastric mixing (Forman 1972).

The musculature of the stomach in frugivorous bats is better developed in the fornix ventricularis, cardiac funnel and region of the pyloric sphincter than in the fundus and

corpus. The muscularis externa is, however, less developed than in the insectivorous species. In addition, small grooves are common on the grater curvature, notably in the megachiropteran *E. wahlbergi*. The decrease in thickness of the muscle layer in frugivorous species, and the development of invaginations, is probably an adaptation to allow distension of the stomach to hold large quantities of food.

Pyloric sphincter

Those species possessing a symmetrical pyloric sphincter have a relatively effective closing mechanism which is of greatest advantage to those bats feeding on a diet difficult to assimilate, such as pulpy plants (FORMAN 1972). The frugivorous and nectarivorous species, *B. cavernarum* and *E. spelaea,* possess a symmetrical valve, while the omnivorous species, *P. hastatus* and *G. soricina,* possess a very long asymmetrical valve. The megachiropteran *E. wahlbergi*, however, has an asymmetrical valve similar to that of *R. leschenaulti* (BHIDE 1980).

The African insectivorous bats appear to possess relatively symmetrical valves, and BHIDE (1980) reported that the aperture of the pyloric sphincter in *M. schreibersi* is central. However, many (partially) carnivorous North American bats exhibit some degree of asymmetry of the pyloric sphincter (FORMAN 1972).

Scanning electron microscopy

The presence of microvilli in the stomachs of insectivorous and frugivorous bats has not been reported previously. The microvilli of *E. wahlbergi*, found throughout the stomach, are long, slender and very abundant. The microvilli of the small intestine of *Rousettus aegyptiacus* have been similarly described (KEEGAN and MODINGER 1979). Villi in the small intestine maximise the absorptive surface area (BARRY 1976), and probably account for the rapid digestive process found in megachiropteran fruit bats (KEEGAN and MODINGER 1979; TEDMAN and HALL 1985 a, b). The microvilli in the stomach of *M. schreibersi,* although much shorter and less abundant than in *E. wahlbergi*, likely serve the same function. In the frugivorous bats, gastric microvilli probably increase the surface area for the absorption of carbohydrates, but, in the insectivorous bats, it is likely they function in maximising absorption of glycogen.

The presence of numerous yeast and fungal spores in the stomach of *E. wahlbergi* is not surprising but their occurrence in all the African insectivorous bats examined is intriguing. The bats may ingest spores when feeding on insects, which might themselves have fed on fruit or flowers.

The absence of symbiotic protozoans and bacteria can be explained by the high food transit rate observed in bats (THEDMAN and HALL 1985a) and the fact that herbivory in bats has not been recorded (YALDEN and MORRIS 1975).

Within the family Phyllostomatidae, a gradation exists from insectivorous to omnivorous (*P. hastatus* to *G. spelaea*) to frugivorous habits (*Artibeus* sp.). Dietary differences habe caused a progressive alteration of stomach structure, from the simplified condition in the insectivorous species, to greater elongation and compartmentalisation of the stomach, culminating in the condition found in *Artibeus* sp. This sequence suggests that changes in food habits from the early insectivorous condition resulted in adaptive modifications to stomach morphology.

The uniformity of gross stomach morphology in the four insectivorous species examined in this study lends support to KAMIYA and PIRLOT's (1975) findings of limited variation in gastric structure between insect-eating bats. Variations between frugivorous bats were, however, much greater. The general trend for frugivorous bats, which ingest large quantities of bulky plant material with reduced protein content, is to increase gastric

volume by elongation and sacculation of the stomach, thereby increasing the exposure of food to the digestive processes.

The stomach of the pteropodid *E. spelaea* exhibits the most specialised form of all the bat species examined. This supports KAMIYA and PIRLOT's (1975) hypothesis that the Pteropodidae followed an independent evolutionary lineage after having diverged from an ancestral stock at a very early stage. The general hypothesis that insectivorous bats constitute the more plesiomorphic taxon (by having a simple tubular stomach), and that the frugivorous species (possessing a complex sacculated gastric structure) represent a more apomorphic taxon, is supported by this study.

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Zusammenfassung

Vorläufige Befunde zur vergleichenden Magenmorphologie von ausgewählten Altwelt- und Neuwelt-Fledermäusen

Mägen von zehn Fledermausarten (acht Microchiropteren und zwei Megachiropteren) aus neun Gattungen und fünf Familien wurden morphologisch und histologisch untersucht. Alle Mägen waren vollständig mit Drüsenepithel ausgekleidet. Es ließen sich aber morphologische Unterschiede zwischen insektenfressenden, allesfressenden und fruchtfressenden Arten nachweisen. Anatomische Abweichungen der Magenschleimhaut waren unter diesen Arten nur gering. Die insektenfressenden Fledermäuse wiesen geringfügige zwischenartliche Unterschiede auf und hatten einen einfachen röhrenförmigen Magen. Die Mägen der Fruchtfresser waren spezialisierter mit stärker voneinander abgesetzten Abteilungen. Rasterelektronenmikroskopische Untersuchungen wiesen das Auftreten von Microvilli in den Mägen einer insektenfressenden und auch einer fruchtfressenden Art nach.

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Social relations in groups of Black-capped capuchin monkeys, (*Cebus apella*) in captivity: sibling relations from the second to the fifth year of life

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Abstract

For juvenile black-capped capuchin monkeys brothers and sisters (related through the mother) are, after the mother herself, the most attractive social partners to one another within the social group. They approach, are approached, and sit together with their respective brothers or sisters significantly more often than with other members of the social group, irrespective of age and sex. The same is true for grooming and social play. In addition juveniles are more interested in their same-sex siblings than in their opposite-sex siblings.

Introduction

Long-term studies of some primate species living in large social groups reveal that, after the mother, juveniles prefer siblings as their social partners. Generally, close kin are more attractive as social partners than lesser or non-related individuals. This is true for *Macaca mulatta* (SADE 1965; DRICKAMER 1976; KAPLAN 1978; CHEPKO-SADE and SADE 1979; BERMAN 1982), *Macaca nemestrina* (MASSEY 1977; WADE 1979), *Macaca fuscata* (KURLAND 1977; GLICK et al. 1986a, b), *Macaca arctoides* (ESTRADA and SANDOVAL 1977), *Macaca fascicularis* (DE WAAL 1977; WELKER and LÜHRMANN 1982a, b; WELKER and WITT 1982), and *Theropithecus gelada* (DUNBAR 1978, 1980, 1982). It has been suggested that such a preference is widespread throughout the primate order (WELKER 1985), including prosimians (TAYLOR and SUSSMANN 1985). This assumption needs to be tested, particularly in New World monkeys, in which there are no comparable studies to date. Previous reports on our long-term study of black-capped capuchin monkeys, indicated that, after the mother, siblings are the most attractive social partners for infants (WELKER et al. 1987, 1990a).

Since we have shown that black-capped capuchin young, irrespective of age, prefer their mothers as social partners (WELKER et al. 1992), we would expect this to apply as well to their second choice of siblings as preferred social partners. Whether any preference for siblings as social partners remains stable or decreases with age, is of particular interest. It is also of importance to establish whether the choice of siblings as social partners is stronger for same-sexed than for opposite-sexed siblings.

Material and methods

The main subjects of the present study were 18 *Cebus apella* juveniles, nine males and nine females, born into the same social group at the primate station of Kassel University. During the period of time under consideration, this group consisted of up to 43 individuals. These 18 subjects provided data on 53 dyadic relationships – 12 male-male dyads, 15 female-female dyads and 26 male-female dyads in none of which the focal animal was younger than two or older than 5 years. The data were collected by focal animal observations (12 animals) or group observations (6 animals). Each focal animal was

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observed daily for 15 minutes each minute being a separate entity such that if one behaviour pattern lasted 10 minutes it was scored 10 times. Group observations were conducted daily for 60 minutes each two minutes being regarded as a separate unit such that if one behaviour pattern lasted for 10 minutes it was scored 5 times. All observation sessions were conducted randomly during the period from 1500 to 1900 hours according to an established schedule. As in a previous paper (Welker et al. 1992) both data sets were combined since comparison between both methods revealed no differences between the different age/sex groups when frequency scores were converted to percentages.

Three of the 18 main subjects were observed over the whole life span covered in this paper, i.e., from year 2 to year 5. All other subjects were observed for from one to three years.

The patterns of social behaviour which occurred regularly and which were scored in terms of their frequency of occurrence per unit time, by trained observers, were the same as those reported previously (Welker et al. 1992). These were: active approach, passive approach (being approached), contact sitting, active grooming, passive grooming, social play.

The frequency of occurrence of a particular behaviour, in which a given sibling was involved with a brother or sister, was converted to a percentage for the purpose of statistical comparison with the same behaviour in which the sibling was involved with other members of the social group on the basis of an expected percentage frequency that assumed that all members of the group except the mother are equally attractive as social partners.

High percentages in the figure should be read with caution since they may represent absolute frequencies of behaviours that occur very seldom compared to others. To give sample sizes for the data sets the mean (with standard error) of the absolute frequency of the different behaviour patterns protocolled within one year is added (Tab. 1).

The statistical test used was the Mann-Whitney test with the level of statistical significance set at $p < 0.05$. The data of one individual collected over one year were taken as one independent sample for statistical purposes.

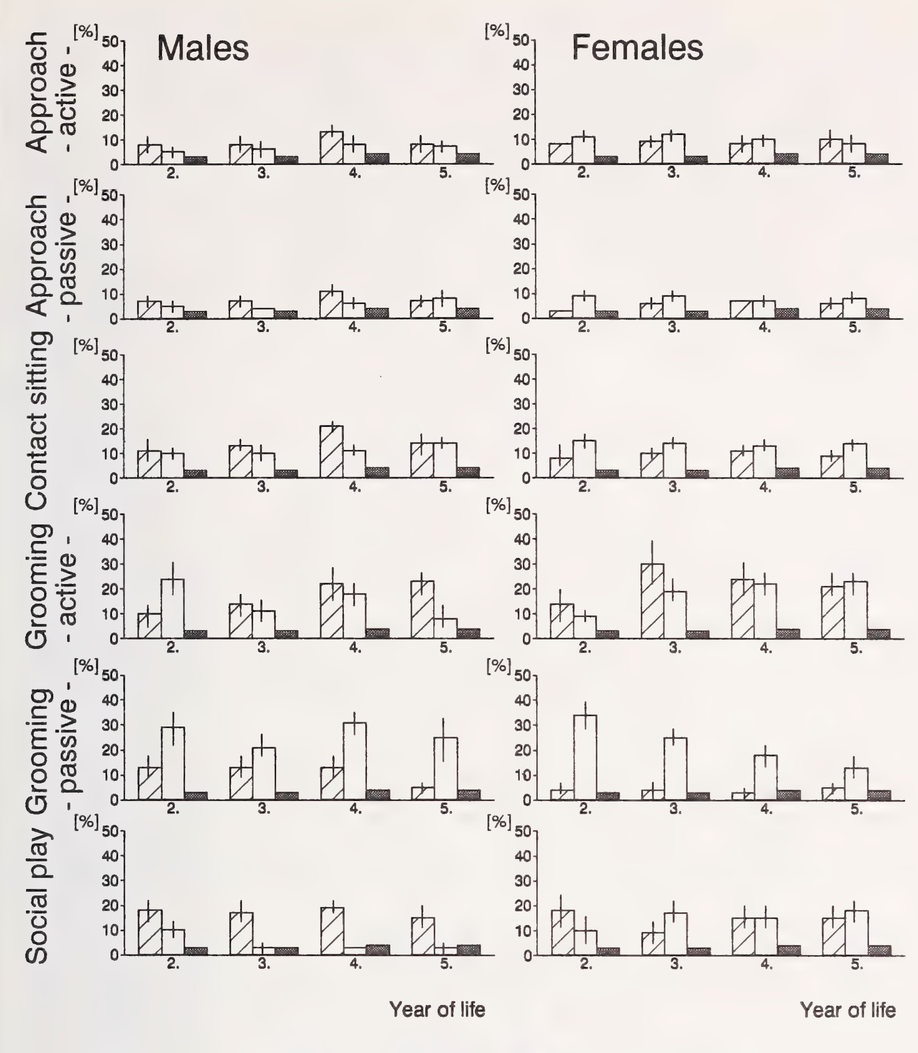
Results

Both males and females approach their brothers and sisters significantly more often than would be expected on the basis of chance alone (approach – active – in the Figure). For males this is supported statistically, from year 2 to year 5, for both their brothers (B/B) and their sisters (B/S) (Year 2, B/B $p < 0.01$ and B/S $p < 0.025$; Year 3, BB $p < 0.005$ and B/S $p < 0.005$; Year 4, B/B $p < 0.001$ and B/S $p < 0.005$; Year 5, B/B $p < 0.05$ and B/S $p < 0.05$). For females this is supported statistically for their sisters (S/S) from year 2 and for their brothers (S/B) from year 3 (Year 2, S/S $p < 0.005$; Year 3, S/S $p < 0.005$ and S/B $p < 0.005$; Year 4, S/S $p < 0.001$ and S/B $p < 0.001$; Year 5, S/S $p < 0.001$ and S/B $p < 0.001$).

As would be expected both male and female juveniles are approached (approach – passive – in the Figure) statistically more frequently by their brothers and sisters than would be expected on the basis of chance. This is true for nearly all possible dyads (for males: Year 2, B/B $p < 0.05$; Year 3, B/B $p < 0.025$ and B/S $p < 0.05$; Year 4, B/B $p < 0.001$ and B/S $p < 0.05$; Year 5, B/S $p < 0.05$; for females: Year 2, S/S $p < 0.005$; Year 3, S/S $p < 0.005$ and S/B $p < 0.005$; Year 4, S/S $p < 0.01$ and S/B $p < 0.001$; Year 5, S/S $p < 0.001$ and S/B $p < 0.001$).

The tendency for juveniles of either sex to choose their own siblings with whom to sit in close contact is even stronger than the behaviour patterns of approaching and being approached. Juvenile males and females sit in close bodily contact (contact sitting, Figure) with their brothers and sisters more often than would be expected on the basis of chance (males: Year 2, B/B $p < 0.01$ and B/S $p < 0.01$; Year 3, B/B $p < 0.001$ and B/S $p < 0.01$; Year 4, B/B $p < 0.001$ and B/S $p < 0.005$; Year 5, B/B $p < 0.05$ and B/S $p < 0.05$: females: Year 2, S/B $p < 0.05$ and S/S $p < 0.005$; Year 3, S/B $p < 0.005$ and S/S $p < 0.001$; Year 4, S/B $p < 0.01$ and S/S $p < 0.001$; Year 5, S/B $p < 0.001$ and S/S $p < 0.001$).

The Table clearly shows that the actual incidence of grooming between juvenile siblings, at least in respect of males, is so low that conversion into percentages, as illustrated in the Figure (grooming – active –), is misleading and statistical tests confirm that, in males, the choice of siblings as grooming partners, in preference to other members



Mean percentage of the frequency of occurrence of some selected behaviour patterns, together with the Standard Error of the Mean, of males toward their siblings (on the left hand side) and of females towards their siblings (on the right hand side), compared to an expected mean frequency based on the assumption that all members of the group are equally preferrable as social partners

of the social group, is insignificant. In females, on the other hand not only does grooming become important from Year 3 but male siblings become particularly important as groomees. Because of high individual differences statistics reveal that for female juveniles, from year 3 on, only their choice of sisters as groomees is significantly greater than their choice of other members of the social group (Year 3, $p < 0.05$; Year 4, $p < 0.001$: Year 5, $p < 0.05$). Male siblings only become attractive as groomees to female juveniles from Year 5 ($p < 0.05$).

As the data for Active Grooming suggests, both male and female juveniles are groomed (grooming – passive –, Figure) more frequently by their siblings, particularly their sisters,

Mean absolute values of the social relations among capuchin monkey mother-related offsprings

Behaviour pattern	Year of life	Sex	Brother	Sister
			(number of dyads)	
Approach active	2.	m	134 ± 19 (6)	91 ± 10 (10)
		f	50 (1)	132 ± 29 (5)
	3.	m	130 ± 23 (9)	85 ± 21 (11)
		f	64 ± 26 (5)	132 ± 43 (5)
	4.	m	111 ± 17 (7)	79 ± 15 (6)
		f	79 ± 20 (8)	70 ± 24 (8)
	5.	m	135 ± 37 (5)	33 ± 6 (3)
		f	91 ± 10 (9)	77 ± 22 (9)
Approach passive	2.	m	137 ± 23 (6)	105 ± 16 (10)
		f	13 (1)	91 ± 32 (5)
	3.	m	132 ± 25 (9)	73 ± 15 (11)
		f	60 ± 21 (5)	112 ± 32 (5)
	4.	m	127 ± 25 (7)	82 ± 15 (6)
		f	92 ± 24 (8)	63 ± 23 (8)
	5.	m	122 ± 28 (5)	50 ± 17 (3)
		f	100 ± 24 (9)	73 ± 21 (9)
Contact-sitting	2.	m	138 ± 42 (6)	116 ± 34 (11)
		f	216 ± 141 (3)	360 ± 89 (6)
	3.	m	221 ± 57 (9)	178 ± 41 (11)
		f	141 ± 42 (5)	202 ± 47 (9)
	4.	m	488 ± 112 (7)	240 ± 65 (6)
		f	197 ± 47 (8)	275 ± 63 (10)
	5.	m	114 ± 43 (5)	479 ± 54 (3)
		f	164 ± 40 (9)	252 ± 45 (9)
Grooming active	2.	m	3 ± 1 (6)	6 ± 3 (11)
		f	9 ± 7 (3)	6 ± 1 (6)
	3.	m	9 ± 4 (9)	8 ± 3 (11)
		f	70 ± 43 (5)	32 ± 12 (9)
	4.	m	11 ± 5 (7)	7 ± 2 (6)
		f	73 ± 30 (8)	60 ± 17 (10)
	5.	m	18 ± 7 (5)	7 ± 3 (3)
		f	78 ± 25 (9)	71 ± 24 (9)
Grooming passive	2.	m	15 ± 6 (6)	38 ± 9 (11)
		f	9 ± 9 (3)	89 ± 20 (6)
	3.	m	21 ± 8 (9)	30 ± 8 (11)
		f	6 ± 4 (5)	33 ± 9 (9)
	4.	m	23 ± 15 (7)	25 ± 3 (6)
		f	4 ± 1 (8)	26 ± 11 (10)
	5.	m	5 ± 2 (5)	52 ± 25 (3)
		f	5 ± 2 (9)	19 ± 4 (9)
Social play	2.	m	168 ± 55 (6)	41 ± 12 (11)
		f	58 ± 22 (3)	87 ± 39 (6)
	3.	m	144 ± 35 (9)	23 ± 8 (11)
		f	75 ± 24 (5)	108 ± 32 (9)
	4.	m	207 ± 45 (7)	17 ± 7 (6)
		f	98 ± 18 (8)	105 ± 33 (10)
	5.	m	91 ± 29 (5)	23 ± 23 (3)
		f	43 ± 8 (9)	70 ± 24 (9)

at all ages levels under consideration. Males are groomed by their sisters (Year 2, $p < 0.001$; Year 3, $p < 0.025$; Year 4, $p < 0.025$) and females by their sisters (Year 2, $p < 0.005$; Year 3, $p < 0.01$; Year 4, $p < 0.05$; Year 5, $p < 0.001$) significantly more frequently than by other members of the social group. Only at Year 3 are males groomed significantly more frequently by their brothers than by other members of the social group

other than their sisters ($p < 0.05$). In contrast, females are seldom groomed by their brothers, in fact, significantly less frequently than they are groomed by their sisters (Year 2, $p < 0.05$; Year 3, $p < 0.025$; Year 4, $p < 0.005$; Year 5, $p < 0.01$).

Finally, with regard to social play (social play, Figure), males play with their brothers, but not with their sisters or other members of the group, more frequently than would be expected on the basis of chance (Year 2, $p < 0.005$; Year 3, $p < 0.001$; Year 4, $p < 0.001$; Year 5, $p < 0.005$). Females, however, play significantly more frequently with their siblings of either sex than with other members of the group (Year 2, S/S $p < 0.05$; Year 3, S/S $p < 0.005$; Year 4, S/B $p < 0.025$ and S/S $p < 0.001$; Year 5, S/B $p < 0.05$ and S/S $p < 0.005$). For both males and females there is a preference for their own sex as play partners (Table).

Discussion

For male and female black-capped capuchin juveniles brothers and sisters are important social partners extending even into adulthood. Together with data on sibling relations in the first year of life (WELKER et al. 1987, 1990a) a social network involving juveniles is apparent. Males prefer their brothers as play partners while females have an equal preference for brothers and sisters. Females have more affiliative contacts (contact sitting and grooming) with their siblings than do males. Similar results on sex-typical differences in juveniles are well documented within the primate order as a whole (for a review see WELKER 1985). Males show a strong preference for their brothers as social partners, while females show an equally strong preference for brothers and sisters, at all age levels. Data on one hand-reared female (WELKER et al. 1990b) suggest that precise genetic relatedness is not the sole criterion for social preference. All group-born, juvenile capuchin monkeys reared by their own mothers, interact more frequently with their siblings irrespective of age and irrespective of paternity. There are no reasons for believing that capuchin monkeys are able to make social distinctions as a function of degree of genetic relatedness.

The above data suggest that kin relationships are important for social cohesion in capuchin monkeys in the wild, as they are in Old World monkeys, and offer a pointer to social relationships in other New World monkeys living under similar group conditions.

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Zusammenfassung

Soziale Beziehungen in Gruppen des Gehaubten Kapuzineraffen (Cebus apella) in Gefangenschaft: Beziehungen zwischen Geschwistern vom zweiten bis zum fünften Lebensjahr

Für Jungtiere des gehaubten Kapuzineraffen sind neben der Mutter (über die Mutter verwandte) Geschwister die attraktivsten Sozialpartner in der Gruppe. Geschwister suchen sich gegenseitig häufiger auf und sitzen häufiger in engem Körperkontakt als mit anderen Gruppenmitgliedern, unabhängig vom Alter und Geschlecht. Entsprechendes gilt für die soziale Körperpflege und das soziale Spiel. Dabei bevorzugen sie gleichgeschlechtliche Geschwister.

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Satellite-linked radio tracking of Atlantic walruses (*Odobenus rosmarus rosmarus*) in northeastern Greenland, 1989–1991

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Abstract

Determined the feasibility of using satellite telemetry for tracking of walruses in studies of stock identities by attaching a total of 12 satellite transmitters to the tusks of male Atlantic walruses (*Odobenus rosmarus rosmarus*) in Dove Bay (approximately 77° N–20° W), NE Greenland in August 1989 and 1990. In 1989 the Platform Terminal Transmitters (PTT) transmitted for an average of 53 days (SD = 36.3; range: 15–111 days; N = 6). In 1990 four PTTs with similar electronics (two of which had a different antenna design) transmitted for an average of 125 days (SD = 96.9; range: 4–238 days). Two different PTTs worked for 62 and 112 days, respectively. It is indicated that the main reason for premature transmission failure is that the walruses dislodged the units. During August and September 1989 and 1990, all walruses regularly made excursions to the west and southwest up to a distance of about 80 km from their terrestrial haul out site on the northern coast of Dove Bay. During late September and early October the formation of a dense cover of land fast ice forced the walruses off-shore into the Greenland Sea. The instrumented animals moved north to winter in leads and cracks in the pack ice between 80° and 82° N off the coast of NE Greenland.

Introduction

In August 1989 and 1990 satellite transmitters (PTTs = Platform Terminal Transmitters) were attached to Atlantic walruses (*Odobenus rosmarus rosmarus*) in Dove Bay, northeastern Greenland. The objective of the study was to determine the feasibility of using satellite telemetry to track individual walruses and thereby potentially determine stock identities; in this case to elucidate whether a connection exists between stocks in eastern Greenland and in the Svalbard – Franz Josef Land region.

Walruses occur in eastern Greenland between approximately 63° N and approximately 81°15′ N, but their main distribution is north of 70° N. Although it has been suggested that walruses in Northeast Greenland form a relatively small and isolated stock, historical information on observations of walruses in the Greenland Sea and the Fram Strait indicates that a connection exists between walruses in eastern Greenland and at Svalbard further east (Born 1990).

Walruses were first instrumented with satellite transmitters by U.S. Fish and Wildlife Service at Round Island in Alaska during the fall of 1987 (Fancy et al. 1988). In Greenland the only terrestrial walrus haul out sites are found within the borders of the National Park in northeastern Greenland. Because the same individuals occur on the beach several times during the open water season, and also in subsequent years (Born 1990), the remote and undisturbed haul out site at Lille Snenæs (Dove Bay) is an ideal place for testing of satellite transmitters in free ranging walruses.

In this study the satellite-linked radio transmitters used in NE Greenland, and their performance, are described. The movements of the instrumented walruses in Dove Bay and the Greenland Sea in the period August 1989 to late March 1991 are also presented.

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Material and methods

In the periods 9 to 24 August 1989 and 6 to 19 August 1990, a total of 12 adult male walruses, *Odobenus rosmarus rosmarus* (six in each season) were immobilized by use of etorphine HCl on the beach of Lille Snenæs (76°52′ N, 19°38′ W) on the northern coast of Dove Bay in NE Greenland, and a satellite-linked radio transmitter (PTT) was attached to the tusk of each animal.

The PTTs transmitted via the ARGOS DCLS system (Fancy et al. 1988; Argos 1989; Keating et al. 1990). At 77° N there are about 28 satellite overpasses during each 24 hour period and the total cumulative visibility of the two satellites above the horizon is about 5.5 hours, with maximum satellite coverage employing the longest satellite passes between approximately 12 and 23 GMT (Fancy et al. 1988).

Three types of PTTs differing in shape, material, antenna type and electronics were used. In 1989 and 1990 a total of eight ST-3 PTTs (Telonics, Arizona, USA) with 20 cm long antennas constructed of multistranded stainless steel cable were attached. Two ST-3 PTTs which were similar in shape and material but had a 7 cm long helical antenna were used in 1990 (Fig. 1). Additionally, two T-2028 satellite transmitters manufactured by Toyocom Inc. (Tokyo, Japan) were attached in 1990 (Fig. 2). The antennas of all transmitters used in 1990 were covered along their entire length by a 0.5–1.0 cm thick layer of urethane (Sikaflex 11 FC) to provide strength.

The PTTs had different duty cycles (Tab. 1). The ST-3 PTTs which had a power output of 1 W had repetition rates of 70 and 77. Repetition rate of the T-2028 units was 60; power output was 0.5 W. None of the PTTs transmitted when two external conductivity electrodes (salt water switch, SWS), positioned on the top of the PTT were connected via sea water (i.e. the walrus was submerged).

In addition to providing locations, the ST-3 PTTs also recorded information on external temperature, duration of the previous dive before an uplink, average dive time over the past 24 or 6 hours, respectively, and number of dives (based on closures of the SWS) during the same periods of time. The T-2028 PTTs gave location but had no memory for storing information of the activity of the SWS.

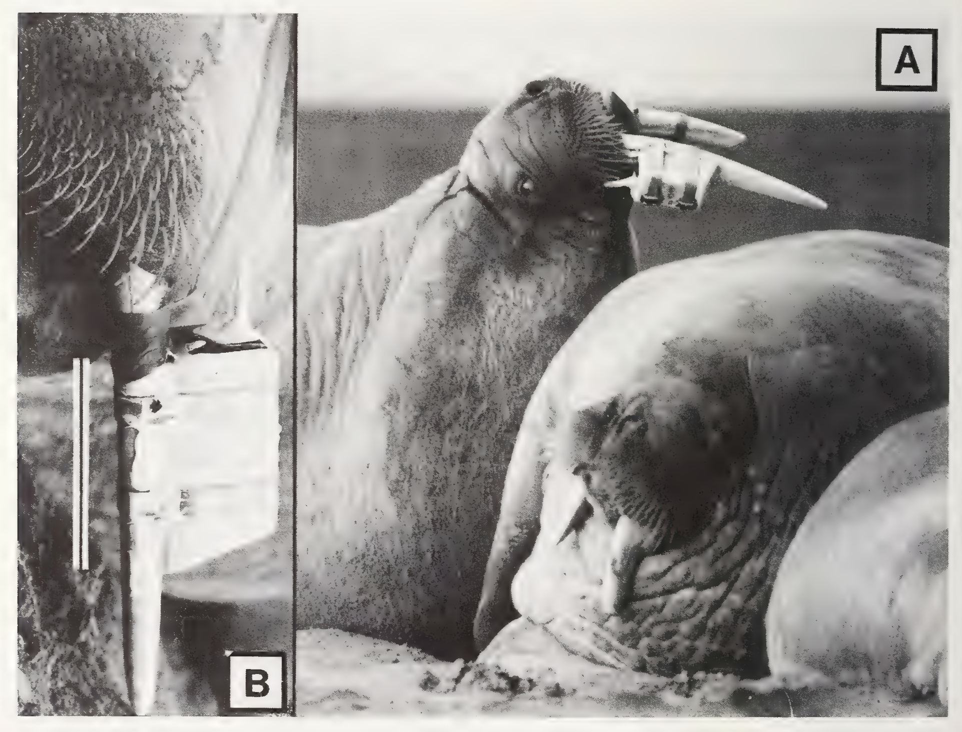


Fig. 1. The ST-3 satellite transmitter with short helical antenna used in 1990 (A); close up view (B); scale = 15 cm. The electronic package and the batteries of the transmitter were encased in a tinned brass housing which was hermetically sealed and backfilled with a polymer material. The housing was covered with urethane rubber to serve as a shock buffer. The unit weighed 1.5 kg

Two 19 mm wide, 316-type stainless steel bandings (Band-It, Houdaille, Denver) were used to attach the unit to the tusk. Grooves were filed in the tusks where these bands would sit, and the lateral surface of the tusk was ground with coarse sandpaper and then cleaned with acetaldehyde. In 1990 polyurethane (Sikaflex 11 FC) was used as a glue between the PTT and the tusk. To ensure that the SWS was out of the water during surfacing, the transmitters were positioned as far up the tusks as possible and somewhat latero-caudally so that they did not protrude in front of the leading edge of the tusks (Figs. 1 and 2). Thereby we hoped to prevent disturbance to the walrus when it was rooting with its vibrissae in the sea floor during feeding. All units were painted with white road paint or fluorescent car paint. Places where the paint was worn off during the field season would reveal sites of physical impact.

Information on ice conditions in the study area was gathered from observations at Lille Snenæs, aerial surveys over Dove Bay during the field periods and extracted from NOAA (thermal infrared) satellite imageries.



Fig. 2. The T-2028 satellite transmitter used in 1990 (A); close up view (B); scale = 25 cm. The transmitter which weighed 0.305 kg was glued into a stainless steel cylinder with polyurethane and two-component epoxy glue, resulting in a total weight of the unit of 0.750 kg

Treatment of satellite-derived data

Activity of the SWS and temperature sensor data were used to determine whether an instrumented animal was hauled out. The software protocol repeated a qualified dive time until updated with a new dive time. Therefore, when the value for the duration of the 'last dive' was repeated in the data stream the walrus apparently was not swimming (i.e. it was hauled out). The duration of such a haul out period was defined as the time between the first and the last uplink in a sequence of repeated 'last dive' data. An increase in temperature and reception of locations in the best quality classes (NQ = 1–3) during the same period were regarded as supportive evidence that the animal was hauled out.

The precision of the satellite-derived locations was determined for the instrumented walruses when they were observed on the beach of Lille Snenæs. The exact position (+/−30 m) of the haul out site (76° 52′ 53″ N – 19° 38′ 10″ W) was determined from a 1:250 000 topographic map (Greenland Geological Survey) based on aerial photographs and ground control points.

Swimming speed was calculated for instrumented walruses from straight line distances and time between uplinked locations. Only distances with locations of quality NQ = 1–3 are used for this analysis.

Table 1. **Performance of satellite transmitters attached on the tusks of Atlantic walruses in NE Greenland in August 1989 and 1990**

Year	PTT ID number/ type	Duty cycle	Expected lifetime[a] (days)	Date of instrumentation (Aug.)	Date of last uplink (day/month/year)	No. of days active	% of expected lifetime
1989	4344/ST-3	Continuous	90+	9	23 Aug. 89	15	17
	4345/ST-3	Continuous	90+	12	30 Nov. 89	111	123
	4347/ST-3	24 h on/24 h off	180+	13	29 Oct. 89	78[b]	43
	1858/ST-3	1 week on/1 week off	180+	14	2 Oct. 89	50	28
	1856/ST-3	1 week on/1 week off	180+	19	1 Oct. 89	46[c]	26
	1859/ST-3	1 week on/1 week off	180+	24	12 Sep. 89	20	11
1990	4348/ST-3	Continuous	90+	6	23 Nov. 90	110	122
	4346/ST-3[1]	1 week on/1 week off	180+	7	10 Aug. 90	4	2
	4349/ST-3	Continuous	90+	8	2 Apr. 91	238	264
	1857/ST-3	1 week on/1 week off	180+	19	13 Jan. 91	148	82
	3985/T-2028	1 day on/3 d off	160+	11	11 Oct 90	62	39
	3984/T-2028	1 day on/3 d off	160+	12	1 Dec. 90	112	70

[a] not including prolongation of life time due to function of the salt water switch. – [b] reliable data for 22 consecutive days, then pause until a single string of sensor data was received on 29 October. – [c] reliable data stream until 9 September then pause until 1 October when a single string of sensor data was transmitted. – [1] this animal bent the antenna and apparently damaged it.

Results

During the field periods, when the instrumented animals were observed several times on the beach after feeding excursions, all PTTs stayed in position on the tusks. We saw no attempts to remove the PTTs, and apparently the animals paid little attention to the presence of the units. Apart from being less vulnerable to wear, the short helical antenna on two of the ST-3 units used in 1990 could not touch the lateral vibrissae and therefore was not able to disturb the animal. During the field season the paint on the somewhat bulky ST-3 PTTs was gradually worn off. The wear began on the frontal side, probably indicating that the units were in contact with the substrate during feeding. Signs of wear were not observed on the more elongate and slender T-2028 units.

During August 1990, five of the six walruses which were instrumented in August 1989 were recognized and subsequently seen on the beach several times during the field period. Walrus no. 4345, which transmitted for 111 days in 1989, still had the 1989 PTT in situ whereas the other animal had lost their transmitters. Walrus no. 4345 was immobilized again on 8 August 1990 and provided with a new PTT (no. 4349; Tab. 1). On 28 and 29 August 1991 this walrus was observed on Lille Snenæs with the 1990-PTT intact on the tusk. On the same dates walrus no. 3985 was observed with the T-2028 PTT attached in 1990 on the tusk. The antenna of this unit was broken off. Another animal (ID no. ?) instrumented in 1990 was identified on the beach without the PTT (Søder, pers. comm.).

The PTTs transmitted between 4 and 238 days after attachment (Tab. 1). In the following analyses PTT no. 4346 (1990) is omitted. It only transmitted for the first four days after attachment while the walrus was hauled out on the beach and is therefore considered not to be representative. On average the ST-3 PTTs attached in 1990 functioned three times longer than those used in 1989 (1989): $\bar{x}$ = 53 days, SD = 36.3, N = 6; 1990: $\bar{x}$ = 165 days, SD = 65.7, N = 3; d = 2.749; $P < 0.05$).

During August and September, when the walruses occurred inshore and hauled out on land and ice, at least one location was obtained from the ST-3 transmitters on an average of 77 % (range: 25 % to 100 %) of the PTT-days (i.e. days where the PTT was in the 'on duty' mode). When the walruses moved offshore after September, the number of locations decreased and at least one location was obtained on an average of only 33 % of the PTT-days (range: 14–58 %) during the remaining period. During August–September the two T-2028 PTTs gave at least one location on an average of 32 % of the PTT-days. The corresponding value for the period October–December was 35 %.

This shift in distribution of instrumented animals following a decrease in temperature and formation of land fast ice in Dove Bay, was also reflected in the location-performance index of all transmitters (i.e. number of locations per PTT-day; Tab. 2). The index for

Table 2. **Location-performance index (locations · PTT-day^{-1}) as unweighted averages for two different periods in 1989 and 1990**

(i.e. inshore period in August and September, and offshore period from October until transmission stop)

Year	PTT-type/N	August–September Index (SD) (PTTs[a])	October–onwards Index (SD) (PTTs)
1989	ST-3/6	7.77 (2.37) (6)	5.49 (3.56) (2)
1990	ST-3/3[b]	2.96 (1.22) (3)	1.25 (0.74) (3)
	T-2028/2	1.67 (0.92) (2)	1.05 (0.39) (2)

[a] no. of active PTTs included in the analysis. – [b] no. 4346 which only transmitted for 4 days at the beach was omitted.

August-Steptember for the ST-3 PTTs attached in 1990 was significantly lower than that obtained for the same type of transmitters in 1989 (d = 2.749; $P < 0.05$). This was also the case during October and later months (d = 4.018; $P < 0.05$; Tab. 2). The low location-performance indices obtained from the T-2028 PTTs during both periods in 1990 were not significantly different from those from the 1990 ST-3 transmitters.

Overall, between 60.3 % and 76.6 % of all locations received from the different PTTs were of the least precise category (NQ = 0; Tab. 3). The ST-3 PTTs with short antennas apparently gave relatively more locations in the least precise category (NQ = 0) than the other two types of PTT (Tab. 3). However, this difference was not statistically assured ($P > 0.05$, $X^2 = 12.521$, df = 9).

The number of locations received, and their quality, was to a large extent influenced by the behaviour of the walruses, and in particularly by whether they were in the water or were hauled out on ice or land. The time that instrumented animals hauled out on the beach of Lille Snenæs, as determined by SWS activity, was on average 0.65 h later (SD = 0.95; range: 0.05–2.43 h; N = 6) than actual time determined from direct observations. On average, the recorded time of entering the water was 1.37 h (SD = 1.50; range: 0.05–5.10 h; N = 16) late in comparison with direct observations. Thus, the activity of the SWS can be used to roughly determine haul out activity. For walruses instrumented with ST-3 PTTs a location-performance index was determined for three "behavioural

Table 3. **Distribution of locations in four categories of precision (NQ = 0–3) for three different types of PTTs**

Year	PTT-type/No. of PTTs	No. of locations	% of locations in four different quality classes NQ = 0	1	2	3
1989	ST-3 long antenna/6	1251	60.3	21.4	16.6	1.7
1990	ST-3 long antenna/2	254	60.6	26.8	11.8	0.8
	ST-3 short antenna/2	459	76.6	17.0	5.7	0.7
	T-2028 long antenna/2	56	62.5	26.8	8.9	1.8

categories": 1. in water, 2. hauled out on land, and 3. hauled out on ice. In both seasons, and for all three substrates, there was a tendency for the number of locations per hour to decrease during the period. These trends were, however, not statistically significant and the data were therefore pooled for the two years (Tab. 4). The location-performance index for animals on ice was higher than for animals which hauled out on land. A relatively larger fraction of the locations was of the least precise category (NQ = 0) when the animals were in the water (Tab. 4). Although the location-performance indices of the two "short antenna" PTTs were lower than those obtained from the eight 'long-antenna' ST-3 PTTs, the differences were not statistically significant ($P > 0.05$).

Table 4. **Location-performance index (locations · PTT–h^{-1}) for three different 'substrates' for ST-3 PTTs on walruses during August–November 1989 and August–December 1990**

Year/ No. PTTs	Substrate	Time surveyed[a] (h)	Location-performance index (loc./h)	% of locations in four quality classes (NQ = 0–3) 0	1	2	3
1989/6	Water	3234.56	0.135	89.5	8.6	1.9	0
	Land	649.77	0.580	49.1	28.4	19.1	3.4
	Ice	675.57	0.660	40.8	29.2	28.5	1.5
1990/4	Water	2781.52	0.056	98.0	0.7	1.3	0
	Land	739.40	0.367	56.8	28.8	13.2	1.2
	Ice	342.67	0.391	50.0	38.1	11.2	0.8

[a] during the period a variable number of PTTs with different duty cycles were monitored.

The satellite-derived locations (NQ = 1–3) of walruses hauled out on Lille Snenæs were somewhat less precise than specified by the system (Tab. 5). On average, the locations in the least accurate category (NQ = 0) were between 10 and 12 km off Lille Snenæs.

Satellite derived information on travelling speed indicates that average swimming speed was 4.0 km/h (SD = 4.03). In this study a maximum travelling speed of 16.7 km/h was recorded (Tab. 6).

Movements

Satellite derived information on movements revealed that during August and the first half of September 1989 and 1990, all instrumented walruses made excursions from the beach of Lille Snenæs, to the shallow water areas in the western and southwestern parts of Dove Bay (Fig. 3). Locations in the best quality classes indicate that maximum distance from Lille Snenæs of such excursions was about 80 km. Due to the absence of ice in Dove Bay in August and September 1990, the animals were not able to haul out on ice floes during their feeding excursion. For that reason substantially fewer off-shore locations were obtained in 1990, and hence the walruses movements could not be followed in similar detail.

Table 5. **Precision of locations for three different types of PTTs on walruses which hauled out on the beach of Lille Snenæs (Dove Bay, NE Greenland) in August 1989 and 1990**

PTTtype	Precision (km) of locations in four location classes			
	NQ = 0 Mean (SD) (range) N	1 Mean (SD) (range) N	2 Mean (SD) (range) N	3 Mean (SD) (range) N
ST-3 Long antenna (N = 8)	12.374 (26.501) (0.114–170.690) 90	0.935 (0.861) (0.134–4.276) 51	1.364 (1.197) (0.114–5.428) 31	0.795 (0.035) (0.764–0.832) 3
ST-3 Short antenna (N = 2)	10.211 (15.633) (0.300–84.959) 43	1.131 (1.142) (0.450–4.581) 19	1.089 (0.786) (0.101–2.387) 11	1.101 (–) (0.444–2.203) 2
T-2028 (N = 2)	– – –	0.748 (0.422) (0.447–1.231) 3	– – –	1.034 (–) – 1

Table 6. **Satellite derived information on walrus swimming speed**

Year	Animal ID	Swimming speed (km/h)				
		Mean	SD	Min.	Max.	N
1989	1856	0.75	0.54	0.32	1.51	4
	1858	3.20	2.93	0.44	8.45	14
	4344	4.56	4.23	0.90	14.99	10
	4345	2.35	0.59	1.68	2.76	3
	4347	9.22	4.39	4.53	16.74	6
1990	3985	0.76	–	–	–	1
	1857	0.72	–	–	–	1
Total		4.03	4.03	0.32	16.74	39

In 1989 the last location from Lille Snenæs was obtained from walrus no. 4345 on 19 September. The two animals (no. 1858 and no. 4345) which still had units which transmitted after the first half of September progressively moved south in Dove Bay during the second half of September. Presumably this happened as a response to fast ice being formed in the bay. Walrus no. 4345 spent some time at the shallow water banks at Påskenæsset and at the southwestern shore of Store Koldewey before moving offshore into the Greenland Sea around 17 October (Fig. 4). The locations in the best quality class (NQ = 3) from the shores near Påskenæsset and on the southwestern coast of Store Koldewey indicate that no. 4345 hauled out on land on these locations. During the second half of October and until 29 November, when the last location was received in 1989, walrus no. 4345 occurred off-shore in the Greenland Sea south to a straight line distance of about 430 km from Lille Snenæs (Fig. 4). Locations were obtained from the shear zone between the very dense pack ice over the continental shelf and the more active and loose pack ice further east overlying deeper waters. At the beginning of November the walrus made an excursion to the shallow water ground at the southern shore of Shannon where there was a polynya in 1989. When transmissions ceased at the end of November, walrus no. 4345 had moved northwards against the East Greenland Current to a shallow water bank.

In 1990 the walruses were able to haul out on Lille Snenæs until the beginning of October. The last location from the beach was received from walrus no. 4348 on 5 October 1990. During the first half of October 1990 the walruses were forced by the formation of a

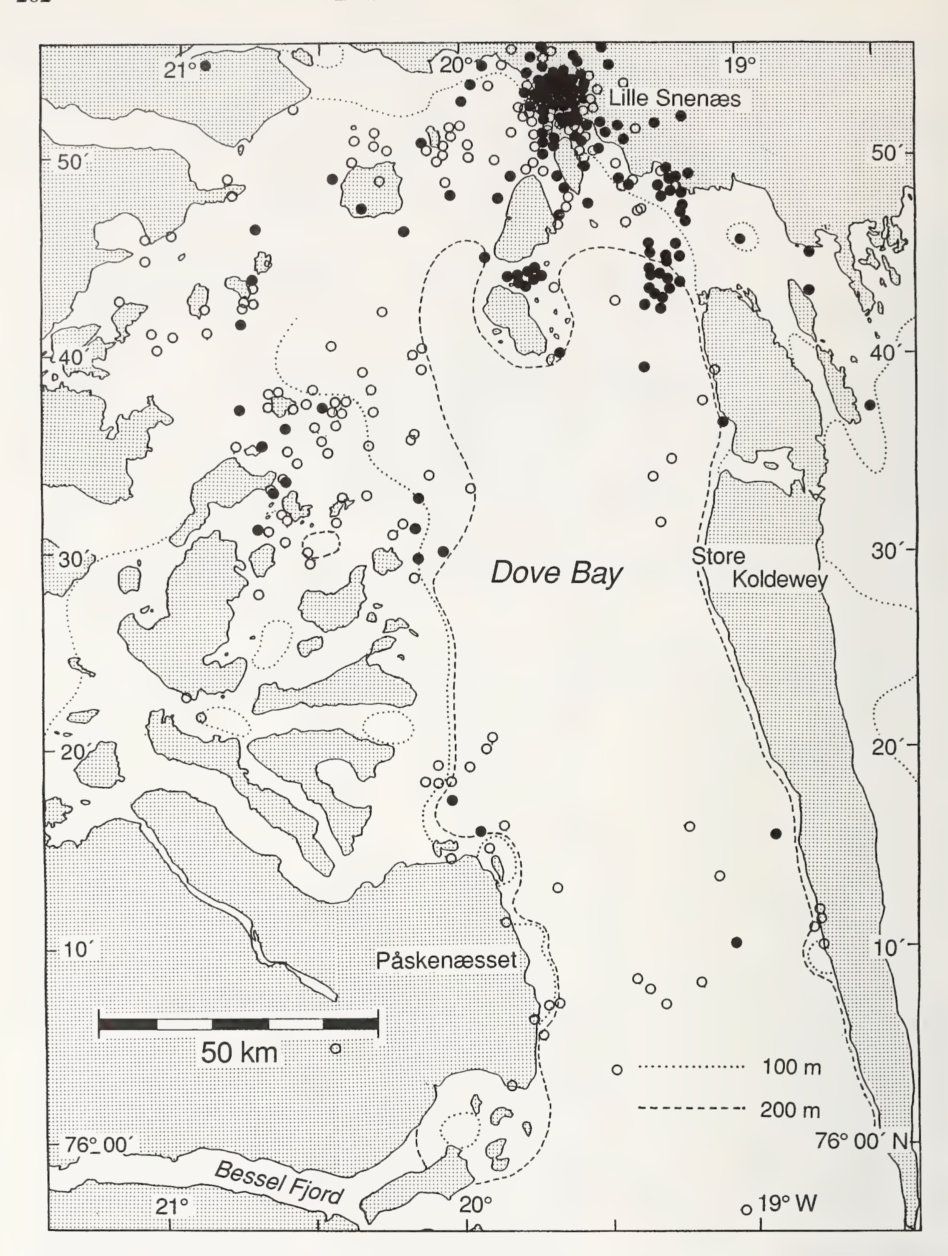


Fig. 3. Locations (NQ = 0–3) received between 6 August and 18 October 1989 (○) and 1990 (●) from a total of 12 male walruses instrumented with satellite transmitters. All locations south of 76° 20′ N were from after 29 September. For days where only locations in the least accurate category (NQ = 0) were obtained, an average location calculated on basis of all locations received during that 24 h period is given as a single point in the Figs. 3–5

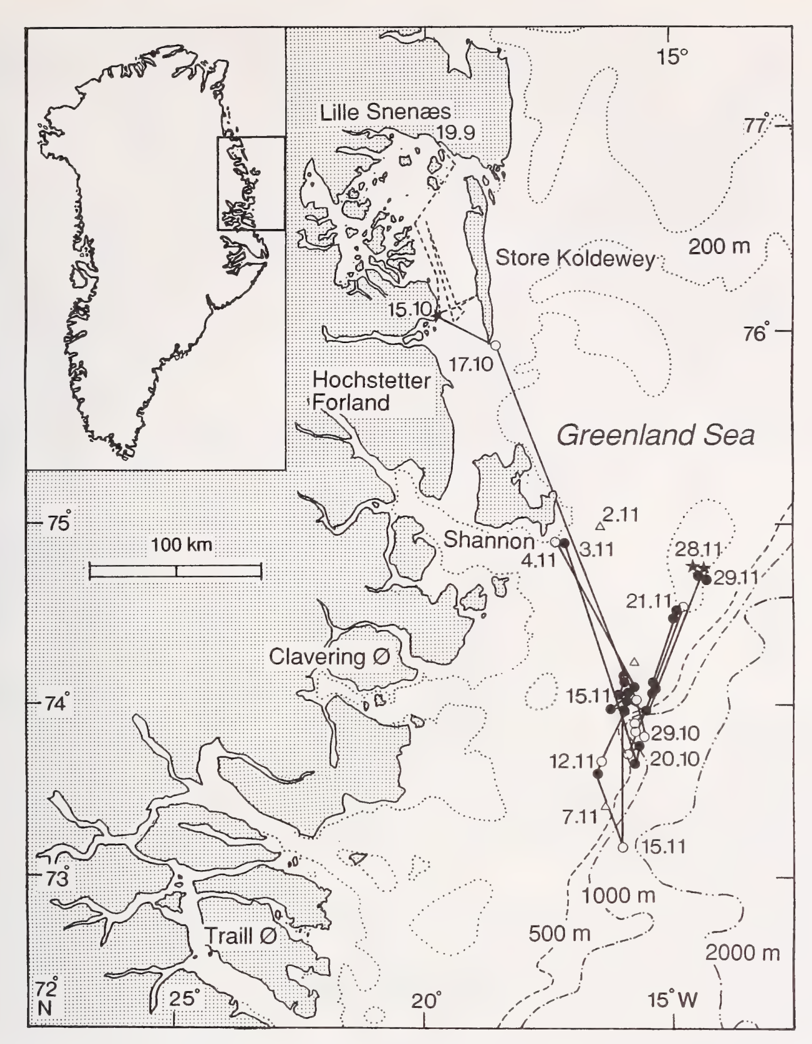


Fig. 4. Movements of walrus "N" (no. 4345) in the Greenland Sea between mid-October and late November 1989. ★ = NQ = 3; ● = 2; ○ = 1; △ = 0, (15.10 = day and month)

dense cover of land fast ice in Dove Bay to retreat offshore into the Greenland Sea (Fig. 5). This emigration occurred both through the straits north and south of the island of Store Koldewey. During the fall migration in 1990 walrus no. 4349 followed more or less the same route as in 1989. In October and November 1990 the instrumented walruses moved north in the Greenland Sea, against the direction of the East Greenland Current. They occurred in the shear zone between the dense land fast ice and the more dynamic pack ice to the east. This zone lies over the edge of the shallow water banks of the continental shelf. On 16 November 1990 walrus no. 4348 occurred at 82° 15′ N and 6° 33′ W (Fig. 5). However, this position represents an average of three locations in the least precise category ranging between 80° 36′–83° 42′ N and 4° 23′–9° 02′ W. The last location from no. 4349 was received on 27 March 1991 (Fig. 5).

The study showed that walruses winter in leads and cracks in the dense pack ice off the coast of NE Greenland and in the polynya off Nordostrundingen ('The Northeast Water').

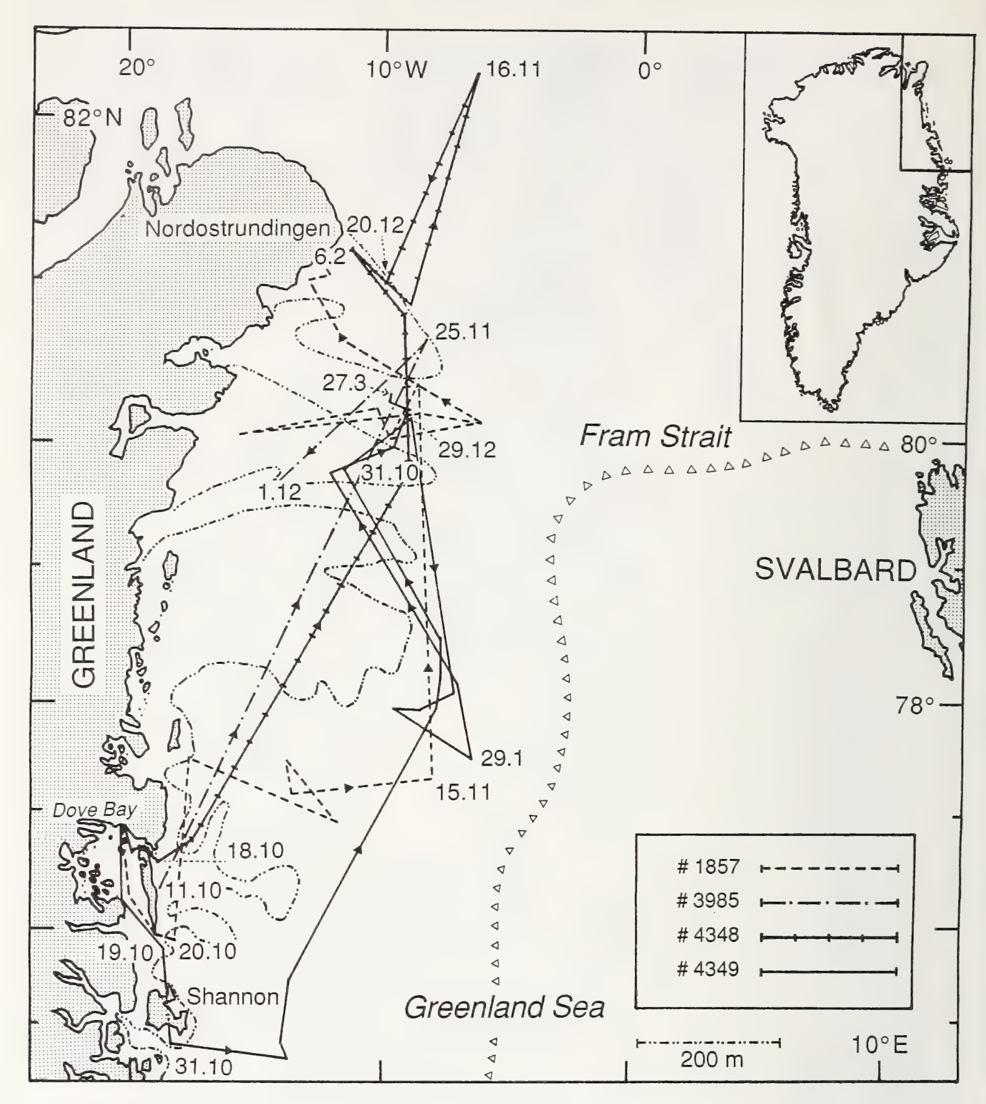


Fig. 5. Movements in the Greenland Sea of four walruses which transmitted after mid-October 1990. △: edge of pack ice late March 1991

Based on tracking of admittedly few animals it is indicated that the group of walruses occurring in eastern Greenland is separate from walruses in the Svalbard and the Franz Josef Land areas further east.

Discussion

Observations at Lille Snenæs indicate that the weight and the shape of the ST-3 PTTs attached to the tusks apparently did not affect the walruses. The ST-3 units represented only about 0.2 % of estimated total body weight of the instrumented animals and 4 to 5 % of the weight of the head (Born, unpubl. data). However, the somewhat bulky configuration of this PTT and the unprotected and lateral position of the 20 cm whip antenna

apparently caused premature transmission failure in some cases. Transmission failure due to breakage or manipulation of the long version of the ST-3 antenna was observed in 1989 and 1990. Loss of the unit after we had left the study area may have caused the transmissions to stop in other cases. This is supported by the finding that walrus no. 4345 (= no. 4349 in 1990), which transmitted for 111 days in 1989 and 238 days in 1990–1991, still had the unit attached when it reappeared at Lille Snenæs in August 1990 and 1991, respectively; and that walrus no. 3984, which transmitted for 112 days in 1990, also had the T-2028 PTT in August 1991 whereas all others had lost their unit. Evidently, the short antenna was superior in that it was not able to touch the vibrissae, which are very sensitive (Kastelein and Gaalen 1988) and thereby motivate the walruses to dislodge the unit. The fact that no wear was observed on the T-2028 PTTs attached in 1990 confirmed our suspicion that the use of smaller and more elongated PTTs is desirable, in particular for the tracking of subadults or female walruses which have slender tusks.

Comparatively more off-shore locations were received during August–September 1989 than in 1990. This is due to a difference in ice conditions in Dove Bay during the two seasons. The availability of suitable ice for hauling out influences walrus behaviour and hence the results of the telemetry. During the field period in 1989 (29 July to 25 August) the central and deeper parts of Dove Bay were 9/10 covered with a sheet of old fast ice whereas the shallow water area in the western part of the bays was 1–5/10 ice covered. In 1990 the sheet of 6–8/10 fast ice which covered the central parts of Dove Bay by 29 July broke up between 6 and 10 August and was swept away by strong winds coming from the west. Thereafter there were no ice floes for hauling out in the area.

The number of locations received per hour was greater for animals on ice than for animals on land. This is presumably because walruses hauling out on land spent proportionally more time doing so during night and early morning than those animals which hauled out on ice (Born, unpubl. data). Hence, walruses on land spend proportionately more time hauled out during periods with reduced satellite coverage and when satellite overpasses occur at low angles. In contrast, walruses which were on ice preferably hauled out during afternoon and evening when there is better satellite coverage. In some cases the 400 to 800 m high mountains in the surrounding of Lille Snenæs may have blocked transmissions during some satellite passes.

Walruses on ice produced a greater proportion of higher quality locations than those on land. Presumably this is due to the combined effect of a difference in diurnal haul out rhythm, as indicated above, and the VSWR (voltage standing wave ratio) effect. When placed on an animal the performance of a PTT is reduced due to the proximity of the antenna to the animal's body and the resulting effect of the VSWR. The result of the VSWR effect is a reduction in effective radiated power from the antenna because of detuning and pattern lobing due to the antenna's close proximity to a large conductive mass (Fancy et al. 1988). We suspect that the VSWR effect may be relatively large for PTTs that are attached to walruses where the antenna is close to the massive and often moist head of the animal. The comparatively poor location-performance index for walruses which were hauled out on land can partly be explained by the VSWR effect also originating from the antenna being in close proximity to the bodies of other walruses. Observations made from Lille Snenæs showed that walruses which hauled out on ice were either single or in groups of only two or three individuals (Born, unpubl. data).

The greater location-performance index of the ST-3 PTTs in comparison with the T-2028 PTTs can likely be ascribed to the greater power output of the ST-3 transmitters.

Our findings are very similar to those reported by Stewart et al. (1989) who in a study of free ranging harbour seals (*Phoca vitulina richardi*), found that about 60 % of the locations obtained at sea were of poorer quality (NQ = 0) and that the overall accuracy of NQ = 0 locations was about 15 km. Satellite-derived locations obtained for walruses at Lille Snenæs were somewhat less accurate than specified by the system. A similar

discrepancy was also experienced in a study of white whales (*Delphinapterus leucas*) by Martin and Smith (1989) and by Stewart et al. (1989) in harbour seals.

As pointed out by Stewart et al. (1989) the fact that fewer locations are obtained from diving animals makes it likely that locations from feeding areas are under represented. Direct observations showed that walruses which apparently were feeding spent about 85 % of the time submerged (Born 1992). Only few locations can therefore be expected from feeding walruses when they do not have an opportunity to haul out on ice between feeding bouts. This was confirmed when very few locations were obtained from walruses offshore during August and September 1990 when there was no ice in Dove Bay. This was in contrast to 1989 when several locations were obtained from walruses which hauled out on ice at the shallow banks in Dove Bay. Walruses feed on bottom dwelling molluscs (e.g. Fay 1982; Fay and Burns 1988) and must theoretically dive for between 6 and 16 hours per day to meet their daily food requirement. They therefore spend a lot of time at the mollusc banks and the probability of identifying such feeding areas via a relatively large number of locations is greater than in seals which feed pelagically. We believe that the stenophagous feeding behaviour of the walrus allows satellite telemetry to be used for the identification of feeding areas and perhaps also of other areas of ecological importance (e.g. mating areas) in this species.

Satellite derived information on travelling speeds obtained in our study is consistent with other published data. According to Fay (1982) the normal swimming speed of walruses is up to 10 km/h. Fay (1981) states that normal cruising speed is about 7 km/h while the maximum "spring" speed is at least 35 km/h.

Our study indicates that the walruses migrate into Dove Bay during the open water season for two purposes: 1. to feed intensively on the molluscs banks, and 2. to haul out on land at Lille Snenæs between feeding excursions to moult.

From tracking a relatively low number of walruses we tentatively conclude that: 1. satellite telemetry is a suitable method for studying spatial and behavioural ecology of walruses, 2. walruses can winter in small groups in leads and cracks along the coast of NE Greenland in areas with shallow water and 3. a separate stock of walruses may occur in these areas.

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Zusammenfassung

Satelliten-gestützte Telemetrie an Atlantik-Walrossen (Odobenus rosmarus rosmarus) von 1989 bis 1991 im Nordosten Grönlands

Um die Anwendbarkeit von Satelliten-Telemetrie für Studien des Bestandes von Walrossen zu klären, wurden im August 1989 und 1990 insgesamt 12 satellitengestützte Sender an den Stoßzähnen von ausgewachsenen, männlichen Atlantik-Walrossen (*Odobenus rosmarus rosmarus*) angebracht. Die Walrosse befanden sich in der Dove Bucht (77° N–20° W) in NO Grönland. 1989 funktionierten die Sender durchschnittlich an 53 Tagen (min.-max.: 15–111 Tage; N = 6), 1990 vier Sender mit ähnlicher elektronischer Ausstattung im Durchschnitt 125 Tage (min.-max.: 4–238 Tage). Jedoch hatten zwei dieser Sender ein anderes Antennendesign. Die zwei Sender des anderen Fabrikates arbeiteten an 62 bzw. 112 Tagen. Der frühzeitige Transmissionsabbruch ist sehr wahrscheinlich dadurch begründet, daß die Walrosse die Sender zerstört und entfernt hatten. Im August und September 1989 und 1990 unternahmen die mit Sendern versehenen Tiere Exkursionen innerhalb der Dove Bucht, und zwar in

einem Abstand bis zu 80 km von dem Platz, an dem sie an Land gegangen sind an der Nordküste der Bucht. Im Laufe des September/Oktober zwang eine neue, dichte Eisschicht in der Dove Bucht die Walrosse dazu, sich nach Osten ins Grönländische Meer zu begeben. Danach strebten sie in Richtung Norden, wo sie in Spalten im dichten Packeis zwischen 80° N und 82° N vor der nordostgrönländischen Küste überwintern.

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Home range shifts accompanying breeding in the Eastern Chipmunk, *Tamias striatus* (Rodentia: Sciuridae)

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Abstract

Capture-recapture techniques were used to study home ranges of 34 breeding and non-breeding male and female *Tamias striatus* over a nine week period. Results showed that reproductive males were of larger body size and had larger home ranges than non-reproductive males. Females attaining oestrus were also larger than non-reproductive females at the beginning but not at the end of the study. Also, females in oestrus had smaller home ranges than non-oestrus females and, for females that attained oestrus, breeding home ranges were smaller than pre- or post-oestrus home ranges. These results suggest that the breeding behavior of *Tamias* may involve home range adjustments made by both males and females.

Introduction

Mating behavior, availability of food and water resources, and local population density have all been implicated as factors affecting home range size in the eastern chipmunk, *Tamias striatus* (Linnaeus, 1758) (Yerger 1953; Dunford 1970; Forsyth and Smith 1973; Tryon and Synder 1973; Mares et al. 1976; Yahner 1978; Getty 1981a; Bowers et al. 1990). For *Tamias,* permanently located burrows provide a fixed center of activity around which areas usually less than 1 ha (more typically, between 0.08 and 0.60 ha) are utilized on a periodic basis (Blair 1942; Ickes 1974; Elliott 1978). Although substantial overlap in home ranges is common, central core areas are defended against conspecific neighbors (Wolfe 1966; Dunford 1970; Ickes 1974; Yahner 1978; Elliott 1978; Getty 1981b). During the summer breeding period, males usually have home ranges that overlap with and may totally subsume the smaller ranges of females and non-breeding males (Forsyth and Smith 1973). Like many solitary, ground dwelling sciurids, *Tamias* has a polygynous mating system (Emlen and Oring 1977), and the expansion of home ranges by breeding males is a way in which multiple females can be mated (Yahner 1978; Dobson 1984). Breeding females are thought to have home ranges that are not different from that of non-breeding females (e.g., Elliott 1978).

In our studies of *T. striatus* in Virginia, USA, we have documented shifts in home ranges that involve both breeding males and females. Here we describe these shifts. Included are examinations of home range size of breeding and non-breeding individuals, and changes in home ranges of individual females that occur with the onset of oestrus.

Material and methods

Our study was conducted at the Blandy Experimental Farm, a biological field station of the University of Virginia located in the northern Shenandoah Valley at an elevation of 190 m in Clarke County, Virginia, USA (ca. 78°00W, 39°00N). Located in the central portion of the Farm is the 50–60 ha Orland E. White Arboretum that includes over 7,000 mostly large, mature native and exotic trees. Specimen plantings are separated by open fields, and running throughout are more than 2 km of loose

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stone walls that were constructed over 100 years ago from rocks and boulders of dolomite origin. The understory of the Arboretum is mowed regularly. The open, parklike vegetation with a combination of thick canopy, open understory, and stone walls with numerous crevices affording refugia and burrowsites, creates favorable habitat for the eastern chipmunk (for further description of the site see Bowers et al. 1990).

The population of chipmunks residing in the Arboretum was studied by capture/recapture techniques for 9 weeks from 1 June to mid-August, 1988. One-hundred eleven folding, Sherman live traps were placed within 1 m of stone walls at 15 m intervals. Traps were set 3–4 successive days during each of the 9 weeks, using cracked corn as bait, and were checked at dawn and dusk. To lessen mortality due to heat stress, traps were placed in cardboard shelters and closed during afternoons on particularly hot days (> 30 °C). Captured animals were weighed, sexed, fitted with a numbered eartag, and released. Sexual condition of all captured animals was recorded: males as scrotal or non-scrotal; females with swollen or non-swollen vulvas (see Smith and Smith 1975).

We use two measures of home range size: 1. the average distance between capture locations; and 2. the maximum distance between all capture locations. Use of linear estimates of home range size was justified because chipmunks showed strong affinities for the stone walls (i.e., in previous investigations they were rarely captured at traps > 5 m from the walls), producing home ranges that extended along walls and were largely one-dimensional (see Bowers et al. 1990).

Results

Over the 9-week study period more than 3,400 trap nights produced over 400 captures of 58 chipmunks. We restrict our analyses here to only those 34 individuals (10 males and 24 females) captured four or more times. These individuals were captured an average of 10.7 ± 7.4 times each over the summer. During the study perid four of the 10 males, and nine of 24 females attained breeding condition. Females were observed to be in oestrus between 5–14 July. Scrotal males weighed more than non-scrotal males, and animals of both sexes in breeding condition were captured significantly more often than reproductively inactive individuals (Tab. 1). Females that attained oestrus in July weighed less in

Table 1. **Mean (±SD) body weights (in August), number of captures, and the average and maximum distance between trap captures (calculated over the nine-week study period) for breeding and non-breeding male and female *Tamias striatus***

Estimate	Females		Males	
	Breeding (n = 9)	Non-breeding (n = 15)	Breeding (n = 4)	Non-breeding (n = 6)
Body weight (g)	86.1 ± 7.3	86.0 ± 12.1	90.5 ± 6.6	77.2 ± 5.8
Number of captures	12.3 ± 6.5	8.0 ± 6.9	8.5 ± 5.5	7.2 ± 5.4
Mean distance (m)	35.5 ± 21.0	43.7 ± 36.8	77.4 ± 40.1	25.3 ± 23.8
Maximum distance (m)	93.2 ± 54.6	88.2 ± 72.0	160.3 ± 40.2	51.8 ± 43.9

June than did females not entering oestrus (61.4 ± 18.1 g versus 79.3 ± 20.2 g); by August there were no significant differences in body weights for females in these two groups (Tab. 1).

A two-way ANOVA testing for differences in home range size for the entire nine-week study period indicated no significant ($p > 0.10$) sex or breeding condition effect, but a significant sex by reproductive condition interaction (Tab. 2). This interaction is due to males in breeding condition having larger, and females who attained oestrus having smaller home ranges over the summer than sexually inactive individuals (Fig. 1).

These different responses by males and females could reflect behavioral changes associated with contrasting mating behaviors, or alternatively, they could reflect individual differences involving non-breeding factors (quality of home range, etc.; see Bowers and Smith 1979). A more rigorous test would examine changes in home range size for

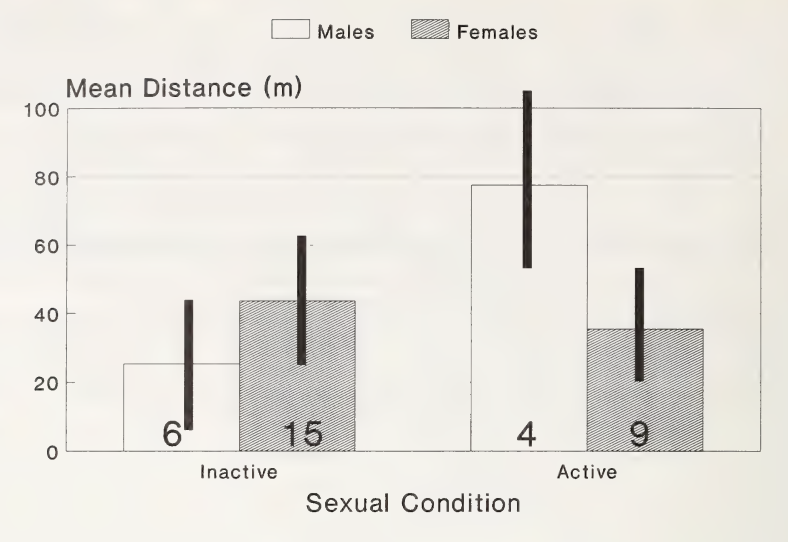


Fig. 1. Mean distance between capture locations (in meters) for breeding and non-breeding males and females. Standard errors of the mean are shown. The number of animals over which averages were calculated are given in each bar

Table 2. **Summary of two-way ANOVA testing for sex by breeding condition differences in the two estimates of home range size**

Source of variation	SS	DF	MS	F	P
Mean distance (m)					
Sex	196.7	1	196.7	0.20	0.66
Breeding condition	772.6	1	772.6	0.77	0.39
Sex by condition	6118.9	1	6118.9	6.06	0.02
Residual	30282.4	30	1009.4		
Total	37389.5	33	1133.0		
Maximum distance (m)					
Sex	126.2	1	126.2	0.03	0.86
Breeding condition	10358.8	1	10358.8	2.80	0.10
Sex by condition	18026.1	1	18026.1	4.85	0.03
Residual	110938.1	30	3697.9		
Total	139508.7	33	4227.5		

particular individuals over breeding and non-breeding periods. Such a test is possible for females who come in and out of oestrus over time periods of between three and nine days (Smith and Smith 1975), and is not possible for males who remain scrotal or non-scrotal for most of the summer months. In our study, nine females bred during the first two weeks of July, while 15 females failed to breed. Comparing home range estimates for individual females captured at least three times during pre-breeding, breeding, and post-breeding periods showed that females attaining oestrus had smaller home ranges during breeding relative to the home ranges of non-breeding females (Fig. 2, a test of difference between breeding and non-breeding chipmunks over the three periods using a repeated measures ANOVA; $F_{2,3} = 17.2$, $P = 0.023$ for mean capture distance; $F_{2,3} = 8.8$, $P = 0.055$ for maximum distance between captures).

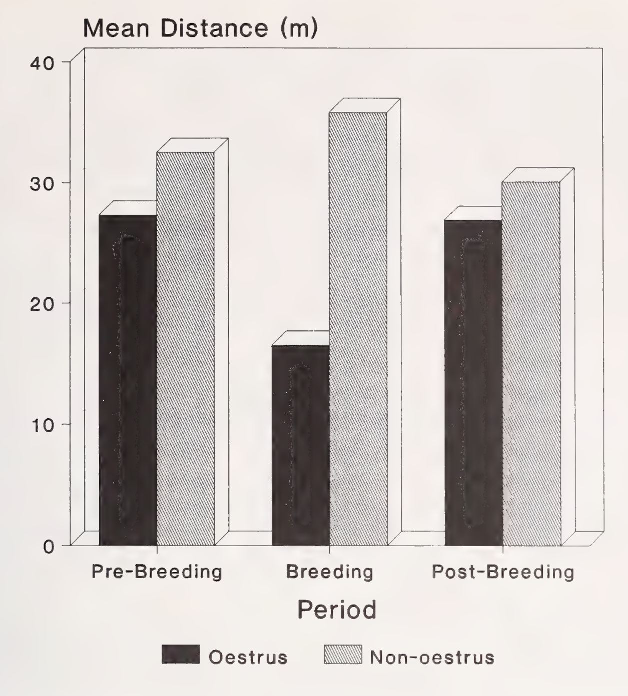


Fig. 2. Mean distance between capture sites (m) for females attaining oestrus (bars with dark shading) versus those that did not (light shading), and broken into three time-periods: i.e., pre-breeding (before 5 July), breeding (5–14 July), and post-breeding (after 14 July) periods. Females entering oestrus had significantly smaller home ranges relative to: 1. non-oestrus females during the breeding period; and 2. home ranges during pre- and post-breeding periods

Discussion

These results add to what is known about polygynous mating systems in solitary sciurids. *Tamias* has two mating periods (i.e. February–April, and early-to-mid July), both which may involve a variable proportion of the resident females (Pidduck and Falls 1973; Smith and Smith 1972; Elliott 1978). In our study females attaining oestrus in July were significantly smaller in June than females not breeding in July. This suggests that summer reproduction was performed by females born in the spring, and that larger females, as a group, may have bred in the spring but not the summer. By August there were no significant size differences between summer breeding and non-breeding females suggesting significant weight gains made by the summer breeders.

Our results also suggest that the reduction in home range size of females accompanying the onset of breeding, while more subtle, may be as indicative of the mating system of *Tamias* as home range expansion by breeding males. It is generally assumed that males expand their home ranges during breeding periods so as to achieve multiple matings (Dobson 1984). During such periods breeding males converge towards home ranges of females in oestrus. This is accomplished through the use of olfactory cues that advertise the onset of oestrus (Dobroruka 1972; Keevin et al. 1981). Successful mating is assured by female tolerance of males in core areas that are usually defended rigorously (Yahner 1978). Limiting movements to certain portions of the home range would further increase the likelihood that breeding males could locate and copulate with resident females. Under

this scenario, reductions in size of home ranges may be a feature of the mating repertoire of female *Tamias* that leads to an increase in competition among males for mates, creating an arena where only the most fit males would breed.

This assumes that the dominant males, in fact, perform the majority of the breedings. However, for the eastern chipmunk a single female may copulate 10–30 times, and with many of the males available (Elliott 1978). Similar breeding systems have been reported for the tassel-eared (Farentinos 1972) and gray squirrels (Horwich 1972). In the former, a majority of the early matings were performed by the dominant males but in the latter there did not appear to be any relationship between dominance and breeding success. If, as Farentinos (1972) argues, the first copulations are most likely to result in fertilization, then reduction in breeding home ranges of females-and the concomitant aggregation of males-would assure that the most fit males do most of the matings irrespective of the total number of males that copulate.

As an alternative, home range reduction by breeding females may result from the harassment by males attempting to copulate. Some authors have noted that up to 12 males may accompany and actively pursue females in oestrus both before and after copulation (Yahner 1978; Elliott 1978). During such mating bouts females may seek refuge from suitors under ground, or in structurally complex microhabitats. Therefore, it may be that reductions in the home ranges of oestrus females result from the aggressiveness of males attempting to mate, and/or is a means by which females in oestrus avoid large male aggregates.

The exact cause of the reduction in breeding female home ranges would be important to the breeding system of the species because in one case females make themselves more available, and in the other, less available to breeding males. Specifically, female adjustments in home range size could either increase the degree to which *Tamias* is polygynous or place severe limits on it. That *Tamias* have highly synchronized oestrus periods could be viewed as evidence supporting the male-avoidence scenario because each female makes herself less available to local males than if oestrus was asynchronous (Emlen and Oring 1977). Further study of the behavior of oestrus females in the presence and absence of breeding males, and the mating success of dominant and subdominant males is needed to distinguish between these alternatives.

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Zusammenfassung

Verschiebungen des Aktionsraumes beim Östlichen Streifenhörnchen Tamias striatus (Rodentia: Sciuridae) während der Fortpflanzung

Die Aktionsräume von 34 reproduktiven und nichtreproduktiven Männchen und Weibchen von *Tamias striatus* wurden über einen Zeitraum von 9 Wochen anhand markierter Wiederfänge bestimmt. Reproduktive Männchen waren größer und hatten größere Aktionsräume als Männchen, die nicht an der Fortpflanzung teilnahmen. Zu Beginn, aber nicht am Ende des Untersuchungszeitraumes waren östrale Weibchen ebenfalls größer als anöstrale. Die Aktionsräume östraler Weibchen waren kleiner als die anöstraler Weibchen, und während des Östrus waren die Aktionsräume kleiner als davor und danach. Die Resultate lassen vermuten, daß Verschiebungen in der Aktionsraumgröße bei beiden Geschlechtern von *Tamias* zur Fortpflanzungsbiologie gehören.

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Aspects of the social behaviour in a captive colony of the Common mole-rat *Cryptomys hottentotus* from South Africa

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Abstract

Qualitative and quantitative behavioural studies on a captive colony of the social mole-rat *Cryptomys hottentotus* are reported. The colony consisted of two castes: reproductives and non-reproductives. The non-reproductives were divisible into "casual workers" and "workers". The amount of work performed was not related to body mass.

Behavioural acts were subdivided into three major categories: Burrow maintenance, interactive and auto behavioural acts. Social interactions were analysed by age and work category. Many of the behaviours appear to be linked to age and not work grouping. Worker groups did not differ significantly in the amount of digging and soil movement undertaken. Juveniles carried food more frequently than adults.

There was a positive correlation between animals initiating and receiving the following interactions: genital allogrooming, sparring, naso-anal interaction and urino-genital sniffing. Juveniles allogroomed the pelage and genitalia of other colony members more frequently than adults. Juveniles sparred and initiated naso-anal interactions significantly more than adults.

There is a distinct toilet area in which the reproductive animals smear-mark significantly more than the other colony members. Smearing of organically derived chemicals may be the mechanism by which chemo-suppression of reproduction is imposed upon other colony members by the reproductives.

Introduction

Cryptomys hottentotus occurs in mesic and semi-arid regions of South Africa (Smithers 1983). The colonies are familial groups comprised of parents and at least two litters and can vary in size from 4 to 18 individuals (Bennett 1988, 1989; Rosenthal et al. 1992). Non-breeding colony members show co-operative and altruistic behaviour in the foraging, storage and subsequent harvesting of geophytes.

Cryptomys hottentotus has a colony structure which lacks working groups based on the relationship between body mass and the amount of work performed.

Studies on the behaviour of the southern African mole-rats were pioneered by Eloff (1951, 1952) who described the basic general behaviour of *Cryptomys hottentotus*. In particular, reference was made to the orientation of the mole-rats within the burrow system and the utilisation of the kinaesthetic senses of these mole-rats in orientation within the burrow system. Generalised behaviours involving digging, feeding and threat postures have been described for *C. hottentotus* and *C. damarensis* (de Graaff 1964, 1972; Genelly 1965). The general behaviour for incomplete colonies of *C. hottentotus* from the Transvaal have been described by Kinloch (1982), but quantitative analysis of the behaviour were not given.

This paper describes, both qualitatively and quantitatively, the behaviours exhibited by a captive colony of field-captured *C. hottentotus*. The various types of social interaction resulting from each behaviour are analysed where possible with respect to the animals' age and work grouping. Where particular actions were uncommon, qualitative behaviour only is reported.

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Material and methods

A colony of 11 mole-rats was captured in May, 1984 at Darling (33° 22′ S, 15° 25′ E) S. W. Cape, South Africa. From the colony of 11, three non-reproductive males were accidently killed on capture leaving only eight mole-rats.

The mole-rats were captured with Hickman live traps (Hickman 1979), or by cutting off their retreat with a hoe when they come to seal opened sections of their burrow system (Jarvis and Sale 1971). They were captured over four consecutive days.

The colony was housed in a transparent Perspex burrow system consisting of three 1-m covered runs (65 mm × 60 mm) linking three transparent chambers which served as nests, toilet areas and food stores. Wood shavings were placed in the chambers, paper towelling and dry grass were provided as nesting material. The mole-rats were fed on a variety of root and green vegetables, apples, grapes and a commercially prepared nutritionally balanced breakfast cereal. The mole-rats drank no free water. The room ranged between 26–28 °C in summer and 18–21 °C in winter. These temperatures were comparable to field temperatures recorded in the superficial foraging burrows (Bennett et al. 1988). The nest chamber was warmed with a lamp to approximately 25 °C, a temperature similar to that recorded in the field, in a burrow leading to the nest in a *C. damarensis* burrow system.

The room was illuminated from a window and consequently received a natural photoperiod. Bathyergids have reduced eyes (Cei 1946; Eloff 1958; Rees 1968) and visual centres in the brain (Hill et al. 1957; Pilleri 1960). *Cryptomys hottentotus* have very small eyes which they keep closed except when alarmed. Eloff (1958) claimed *Bathyergus* and *Cryptomys* could not see, but could detect air currents on the cornea. In the *C. hottentotus* colony under observation, no obvious behavioural response was detected to bright flashes of light or to movement by an observer as long as it was not accompanied by sound or by an air current.

The behaviours of the 8 *C. hottentotus* (2 males and 6 females) trapped at Darling in April 1984 were observed for a total of 240 hours between 15th May and 2nd August, 1984. Colony behaviour was observed daily by means of continuous scans for durations of 2 to 6 hours. The roles of the individuals within the colony were determined over the period 15th May to 2nd August.

All statistics were carried out with the aid of Siegel (1956) and Zar (1984).

The results obtained for many of the behavioural acts were tested statistically to determine if there were significant differences for the age and role of the mole-rats in the colony Darling 1. Sexual differences are not recorded here because there were only two males.

Results

Burrow maintenance behaviours

Four behaviours fall under this heading a) digging and gnawing, b) sweeping and transport of wood shavings in the burrow excluding near the toilet, c) nestbuilding and the carrying of nesting material and d) food carrying. These behaviours are readily quantifiable and are believed to approximate behaviours that occur in the wild (Bennett 1988). In the wild, nest building and the carrying of nesting material involve transporting stripped husks and root epidermis from harvested bulbs, tubers and rootstocks etc. to the nest chamber. These were the only materials found in the nests of wild colonies. In captivity wood-wool was provided for this purpose. In the wild, bulbs, corms and other small food items are carried to the food store and in captivity small items of food were also transported to one clearly identifiable section of the system. The food items were carried between the incisors, the head being held high and the mole-rat moved backwards or forwards with its load.

Based on the type and amount of work performed by individuals and on their reproductive role, the mole-rates in the colony of eight animals were placed into three categories. A reproductive caste and a non-reproductive caste composed of two work-related groups, "workers" and "casual workers" (see Table) (Bennett 1989).

The three workers (w) were the younger, smaller sized mole-rats. They were involved in 12.3 to 22.3 % of the total work done by the colony.

The three casual workers (cw) were usually the larger mole-rats, although a juvenile was ranked within this group. They were involved in 5.5 to 6.8 % of the total work undertaken by the colony.

The two reproductive mole-rats (RF, RM) could not be distinguished from workers or

Analysis of the amount of work performed by members of the Darling 1 colony

Data were collected over four months May to August, 1984. (After BENNETT 1989)

Animal I.D.	Group	Sex	Weight capture April	Weight August	Frequency of digging and soil transport	Total work (N)	% of total work
No. 1001	W	F	28.1	76.1	17	47	12.3
No. 1002	W	F	27.4	87.0	29	51	13.3
No. 1004	W	M	36.0	102.0	51	85	22.3
No. 1007	R.F.	F	55.5	95.0	92	116	30.4
No. 1040	R.M.	M	75.0	131.0	4	13	3.4
No. 1070	C.W.	F	45.0	82.5	19	26	6.8
No. 1008	C.W.	F	59.0	90.0	16	21	5.5
No. 1003	C.W.	F	31.0	66.0	5	22	5.7

W = worker; C.W. = casual worker; R.F. = reproductive female; R.M. = reproductive male; F = female; M = male.

casual workers on the basis of the amount of work undertaken (U = 3, p = 1.20 and p = 1.20, Mann Whitney U-test p = 0.05 level of rejection) but clearly differed from the others in being the only reproductive animals in the colony. The male did little work (3.4 %), but the reproductive female undertook 30.4 %, especially that associated with nestbuilding and sweeping.

There was a significant tendency for workers to maintain the burrows and work more frequently than casual workers (U = 0, p = 0.05 Mann Whitney U-test, 1 tailed test).

Using the Kruskal-Wallis test it was found that the three groups did not differ significantly in the amount of digging and soil movement undertaken ($p = > 0.05$).

There was a significant difference in the frequency of food carrying by the mole-rats ($\chi^2_7 = 22.45$, N = 89; $p = < 0.01$). This was linked to the age of the mole-rat; juveniles carried food significantly more frequently than adults (U = 1.5, p = 0.028, Mann Whitney U-test).

Interactive behaviours

Naso-anal interaction

Naso-anal interactions involve contact between the nasal region and anal region of two animals, lying side by side, head to tail. The behaviour does not lead to sexual activity and is undertaken by all colony members. The animals appear very excited during the activity and vocalisation may occur.

There was a positive correlation (rs = +0.55) between the number of naso-anal interactions initiated by particular animals and those in turn received (Fig. 1). Juveniles initiated significantly more naso-anal interactions than did adults (Mann Whitney U = 0; p = 0.028). Reproductives were rarely involved in naso-anal interactions.

Urino-genital sniffing

One mole-rat sniffs the anal region of another individual which raises its tail and simultaneously emits a series of high pitched squeals whilst jumping with its hind legs with each squeal.

There was a positive correlation (rs = +0.55) between the number of urino-genital sniffing sequences undertaken by particular individuals and the frequency with which they inturn received these interactions (Fig. 1).

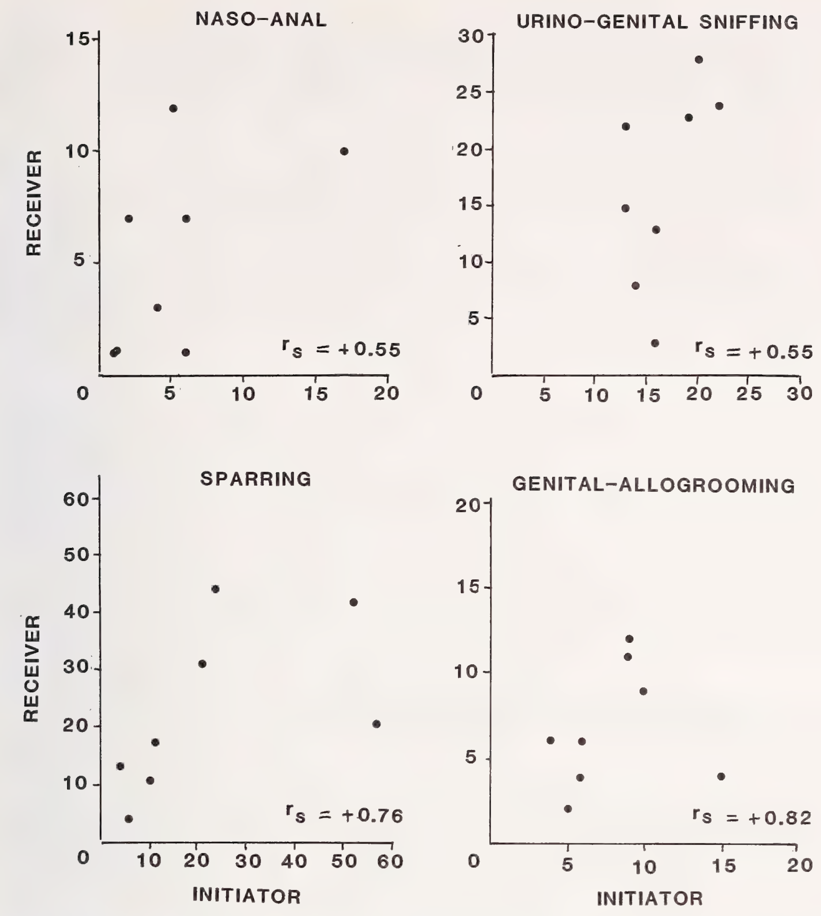


Fig. 1. The Spearman Rank correlations between the frequency of initiating and receiving naso-anal, urino-genital sniffing, sparring and genital-allogrooming behavioural interactions

There was no correlation with the age of the mole-rat (Mann Whitney U = 5; p = 0.486).

Sparring

Sparring consists of 3 types of interactions: Adult-adult, adult-sibling, sibling-sibling interactions. In sparring, two animals gently lock their incisors and then have a tug-of-war. During the tugs-of-war the individuals brace themselves in the burrow with their forefeet and try to pull one another. This may be interspersed with nose-butting and pushing at each others faces with their forefeet. The skin is never bitten and interactions are terminated either by one animal rolling over onto its back and exposing its belly and genitalia or by one animal reversing at high speed along the tunnel system. Adult-sibling and sibling-sibling interactions are common. Whereas adult-adult interactions are infrequent.

A significant positive correlation (rs = +0.76) was found between the number of sparring episodes initiated by particular animals and the frequency with which these animals inturn received sparring interactions (Fig. 1). Juveniles sparred significantly more frequently than did adults (Mann Whitney U = 0; p = 0.028).

Juvenile-juvenile sparring constituted 64 %, adult-adult 7 % and adult-juvenile 29 % of all observed sparring interactions (n = 183). These data suggest that sparring is important in pup development and the subsequent incorporation of pups into the colony.

Tail-pulling

When two animals are moving in the same direction within the burrow, and the anterior male-rat then stops to feed or rest, the posterior male-rat may pull the obstructing individual back along the burrow by its tail. The towed animal usually turns on its back and attempts to brace itself against the sides of the burrow. Once released the mole-rat will often return to the place from which it was initially towed from and tail-pulling may be initiated again.

Passing over

Mole-rats usually passed each other by flattening their bodies and pulling against the mole-rat that they were passing. The mole-rat on top was usually the faster moving individual (unquantified). Before passing, mole-rats would often chirp, especially when passing animals dominant to themselves. Small mole-rats passed side-by-side in the tunnel system.

Passing under

This occurred when one mole-rat passed another by moving underneath it.

Passing side-by-side

This behaviour occurred in the tunnels and is self explanatory.

Biting

Biting occurred when one mole-rat encountered another in the nest, when one animal blocked the path of another, or during a tussle over food. It involved the biting of the tail, leg or rump. The bites varied in intensity from nibbling to a severe bite.

Rump chewing

This behavioural act involves one mole-rat mouthing the fur on a conspecific's rump and then taking the rear between the incisors. The incisors were moved in a gentle chewing action.

Mouthing

When mouthing, one animal would take another's head between its incisors, sometimes moving the mouth in a chewing motion. The aggressor would then often drag the victim along by its head.

Pushing

This behaviour involved a mole-rat pushing its hindlegs against a conspecific whilst bracing itself with the fore legs and raising the head. In this position the mole-rat would move backwards while pushing the other down the tunnel.

Allogrooming

Allogrooming consists of nibbling and ano-genital licking. In "nibbling", the groomer bites gently at the groomee's head, neck, shoulders, flanks or back. In "ano-genital

licking" one animal licks the ano-genital region of another, this may also involve some nibbling of the fur in the ano-genital area. Allogrooming occurs in the nest and usually occurs when a mole-rat has just entered the nest. Grooming is initiated when the groomee is lying in a relaxed position. The groomer moves to the head and thoracic region of the groomee and nibbles at its fur, occasionally another region of the body will be groomed. The groomee responds by moving the part of its body being nibbled towards the groomer it rarely responds by immediately reciprocating the groom. The groomee may however reciprocate-groom the groomer after a short time lapse.

In ano-genital grooming, the groomer usually approaches the groomee from the rear and pushes its nose between the hind legs of the groomee. During ano-genital grooming the groomee gives out a high pitched sibilant twitter and may on occasion thrust its hind legs into the face of the groomer. The fur around the ano-genital area may also be nibbled, but licking occurs 90 % of the time. Ano-genital licking is a short-lived behaviour lasting only a few seconds. Allogrooming around the groomee's mouth and nasal area also occurs frequently.

The two reproductive animals and a casual worker (Nos. 1040, 1007, 1008) autogroomed significantly more frequently than they allogroomed ($p < 0.05$, $N = 299$; S.E. = 0.026, binomial test rejecting at $p = < 0.05$ level). Two workers and a casual worker (Nos. 1001, 1002, 1003) allogroomed more frequently than they autogroomed, whereas one worker and one casual worker (Nos. 1004, 1070) autogroomed and allogroomed with equal frequency. Juveniles allogroom significantly more frequently than adults (Mann Whitney $U = 0$; $p = 0.028$).

There was no significant difference in autogrooming between adults and juveniles (Mann Whitney $U = 6.5$; $p = 0.486$).

With genital allogrooming, however, there was a strong direct correlation ($r_s = +0.82$) between those mole-rats initiating and those in turn receiving grooming to the genitalia (Fig. 1).

There was a significant trend for juveniles to genital allogroom more frequently than adults ($p = 0.0170$, $N = 64$; S.E. = 0.058; Binomial test $p = < 0.05$ level of rejection).

Allocoprophagy

Allocoprophagy is rarely undertaken except by young or juvenile mole-rats. These animals beg faeces from an adult engaged in autocoprophagy. The begging individual approaches the rear or side of the donor, while giving a high pitched mewing noise resembling Sue-Sue-Sue. The mole-rat then pushes its nose between the hind legs of the donor, probes the anus of the donor with its teeth and pulls out faecal material. While this is taking place, the donor produces a high-pitched sibilant cry, similar to that produced by an individual who is being allogroomed in the ano-genital area. Adult mole-rats have been seen eating faeces previously voided by another colony member in the toilet area.

Autobehaviours

Autogrooming

There are three methods of cleaning the coat, namely, scratching with the hind leg, licking and nibbling with the incisors.

Scratching is usually applied to the head, neck, shoulders and flank region, the hind leg moving in a rapid series of arcs and combing the fur on the downbeat. When the head or neck is being groomed the head is tilted to the side of the body with the hind foot being used to scratch. The forefeet brace the mole-rat as it grooms itself.

Licking is used to clean the paws, lower belly and ano-genital area. The animal either

first licks and moistens its paws which are then combed through the fur, or it directly licks its fur using small sweeping movements. In the case of ano-genital licking, slight lapping movements are utilised. When cleaning the belly, the ano-genital region or the toes of the hind feet, the animal rolls backwards and supports its body on the sacral region, its hind legs are splayed out and its forelegs may be used to balance the body. Incisors are groomed by the mole-rat initially licking its paws and subsequently grooming its incisors and nose with the paws. The digits of the hind feet are nibbled and groomed with the incisors.

Tooth-sharpening

The incisors of the bathyergids grow continuously and in the natural environment are worn down as they chisel-tooth-dig through the soil. In captive animals the incisors are worn down and sharpened by tooth-sharpening. Tooth-sharpening usually occurs (96 % of the time) in the nest area. The mole-rat initially braces itself with its forepaws while adopting the normal tooth-sharpening posture. Forward and backward and side to side actions of the lower jaw are then used to file the upper and lower incisors against one another. Squeaky filing noises are produced during these movements. Short forward thrusts of the lower incisors against the upper ones sharpen the lower incisors, whereas longer slower backward movements of the lower incisors across the upper incisors sharpen the upper. Loose flakes and dust of chipped incisor are periodically flicked out ot the mouth by the tongue.

There was a highly significant difference in the frequency of tooth-sharpening episodes between colony members ($\chi^2_7 = 24.56$, N = 367; p = <0.001 Chi-square, one tailed test).

However, this was not related to age (Mann Whitney U = 7; p = 0.886). The score of each individual weighted the statistic, thus animal No. 1004 tooth-sharpened 44 % more frequently than the mean frequency obtained for tooth-sharpening, whereas animal No. 1070 tooth-sharpened 40 % less than average.

Coprophagy

Autocoprophagy commonly follows ano-genital grooming. The animal rolls backwards and supports its weight on its sacral region. Its hind legs are splayed laterally and the animal doubles up. The forelegs of the animal are used to balance and brace the animal. The incisors are used to probe and pull faecal material from a slightly everted anus. The faeces are then eaten. The duration of coprophagy may last a few seconds to many minutes.

Some animals practiced autocoprophagy more often than other individuals ($\chi^2_7 = 35.59$, N = 195; p = <0.001 one tailed test), but this was not related to the age of the mole-rat or its role (Mann Whitney U = 2; p = 0.114). However, the reproductive male engaged in the least amount of autocoprophagy. In this study animals No. 1004 and No. 1040 weight the χ^2 statistic.

Alarm and threat posture

There are essentially two alarm and threat behaviours used in response to disturbances from outside the colony: head-back threat posture and pumping.

In the head-back threat posture, the animal stands with its head thrown back, its eyes open and its mouth fully agape. The forefeet are placed firmly in front of the mole-rat and the hind limbs are widely splayed laterally but braced for a rapid advance or retreat. Periodically the mole-rat snorts and chatters its teeth. The posture is firm and rigid with the animal making short jerks or jumps towards the agonistic source.

Pumping

In pumping, the mole-rat cautiously approaches the source of alarm to threat repeatedly sniffing the air and holding its tail out straight. While still 10–20 cm or more from the source of alarm, the animal stands with its fore and hind legs splayed laterally, its head is stretched out forward and its body flattened dorso-ventrally. The mole-rat then pumps its hind region (legs and sacral area) up and down. This action is quite forcible, especially on the downstroke. In a very high-level threat situation the whole body posterior to the shoulders is lifted off the ground with the upstroke.

A pumping sequence may consists of between six and twenty downstrokes, each sequence is followed by a refractory period, in which the mole-rat first remains very still and then advances a few centimeters closer to the source of aggravation. The pumping display is then repeated. The mole-rat is extremely cautious and may rapidly retreat backwards along the burrow.

General movement in the burrow

Cryptomys hottentotus move backwards and forwards in the burrow system with equal ease. They walk and run along the burrow with their hind legs held far apart with most of the sole of the foot held off the ground. The limbs are short giving them a low body carriage. The head is usually held straight out, but is occasionally slightly lowered. The eyes are kept closed except when investigating a new disturbed or damaged area in the burrow system. The mole-rat then opens its eyes, holds its head held high, sniffs the air and cautiously approaches the area. During this cautious approach the fore and hind feet are braced against the perimeter of the burrow to facilitate rapid retreat.

The mole-rat turns within the burrow system by curving its body and rotating sideways, using its forefeet to do much of the pushing, however, a final thrust is provided by the hind feet.

The mole-rats are generally very agile, the actual speeds with which the animals move in the natural underground system have not been recorded, but mole-rats kept in the laboratory are capable of moving both forwards and backwards, at speeds of up to 15 cm/second.

Cryptomys hottentotus are exceptionally aggressive animals and will bite on capture, this being most noticeable in freshly captured specimens. They are extremely sensitive to air currents which ELOFF (1958) suggests are detected by the cornea of their eyes. A series of short sharp rapid jumping movements with the mouth agape accompanied by grunting sounds are evoked if one blows air into the face of an individual (DE GRAAFF 1964; BENNETT, pers. obs.).

Toilet behaviour

There is a well defined toilet area within the burrow system, usually a blind ending tube that is utilised by all the colony. There are essentially three types of toilet behaviour: Grooming and smearing, urination and defaecation.

Grooming and smearing

In grooming and smearing, the mole-rats may enter the toilet area and not urinate or defecate. This is common in *C. hottentotus*. On entering the toilet area the mole-rat spends time smelling the area and then vigorously grooms its head region, flanks and belly, sometimes the genitalia are also groomed. Before leaving the toilet, the animal kicks back with its hind legs for a few times, and leaves the toilet while dragging its ano-genital region along the burrow. A small amount of fluid (urine?) is left in a trail along the tunnel. This

wet trail is smelt by other colony members as they pass along the marked section of the burrow.

Some animals groomed and smeared within the toilet area significantly more often than other colony members ($\chi^2_7 = 17.41$, N = 138; p = <0.01). This was not linked to the age of the mole-rats (Mann Whitney U = 4; p = 0.342). There appears to be a tendency for the reproductive pair to groom and smear more frequently than the rest of the colony (Mann Whitney U = 0, p = 0.072), although not significant at p = < 0.05 level (Fig. 2).

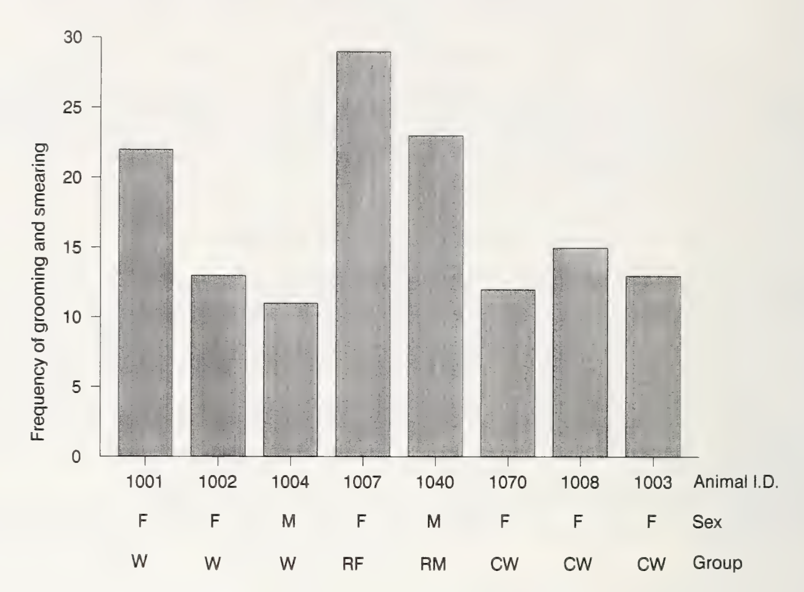


Fig. 2. The relative frequencies of grooming/smearing sequences in the toilet area of a *Cryptomys hottentotus* colony. RM = Reproductive Male; FR = Reproductive Female; CW = Casual Worker; W = Worker; F = Female; M = Male

Urination

Urination usually occurs after an animal has roused from rest or after feeding. The animal moves its hind legs apart, lowers its rear and raises its tail. Short jets of urine are voided. At the end of urination the animal briefly drags its rear along the burrow. A conspecific passing over the drag-marked region sniffs the marked zone and then moves on. Urination is not restricted to a particular site in the system (vs defaecation) and the site appear to be randomly selected.

There was no significant difference between colony members in the frequency of urination ($\chi^2_7 = 7.48$, N = 170; p <0.3 >0.2).

Defaecation

Defaecation occurs after awakening from sleep or after feeding. The mole-rat approaches the toilet area head first and smells it briefly, before reversing out of the toilet area and turning around. The animal then backs into the toilet tube. During defaecation, the mole-rat stands with its hind feet well apart and its tail raised. Its body is held rigid until the pellets are voided. The faeces then are kicked with the hind legs towards the blind end of the toilet area. After defaecating, the mole-rat grooms itself thoroughly starting with its head and finishing at the ano-genital area. In *C. hottentotus* defaecation follows or precedes urination but the two occur in different parts of the burrow system.

Feeding

When feeding the mole-rat squats on its hind feet and holds the food with its forefeet. When feeding on bulbs such as *Oxalis* sp., *Homeria* sp. and *Romulea* sp. the mole-rat grips the bulb between its forepaws and dehusks it, slowly rotating the bulb as it bites off the scaley outer layer. Once the bulb has been dehusked, the mole-rat cuts off and eats small portions of it. Food shaking and brushing precede eating and occur at irregular intervals during feeding. The bulb is occasionally shaken with the fore paws or held in the incisors and brushed with the forefeet. This action dislodges any attached soil.

Discussion

These first in-depth behavioural studies on a captive colony of *C. hottentotus* have provided an opportunity to describe basic colony behaviour in this social bathyergid. This study on *C. hottentotus* provides a comparison with the other social bathyergids which may help elucidate which features in the behavioural repertoire of the social bathyergids evolved first.

Maintenance behaviours

Digging and burrowing

Digging behaviour of all the genera of the bathyergids is very similar, although there are differences in the actual mode of excavation. Digging in all genera is initiated by alternate movements of the forepaws. However when extending the burrow through well packed substrata, the mole-rats of four genera excavate the soil with both the upper and lower incisors, whereas the genus *Bathyergus* utilises its claws and only occasionally its teeth for digging (Genelly 1965; Jarvis 1969; Jarvis, pers. comm.; Bennett, pers. obs.). In *C. hottentotus*, the two major maintenance behaviours (digging and soil movement) are not restricted to particular groups. In contrast, these behaviours are performed mainly by the frequent worker caste in *C. damarensis* (Bennett 1988) and by small-sized workers in *H. glaber* (Jarvis 1981; Lacey and Sherman 1991). Thus, in these behaviours there appears to be a difference between *C. hottentotus* and the two more highly social bathyergids.

Carrying food

In the burrow system much of the food encountered by the mole-rats while digging is carried to the food chamber. The mode of transportation varies with the size and nature of the food. The social species store food in a common food store the animals actively involved in foraging will probably also collect, transport and store the food. In *C. hottentotus*, juveniles (workers) carry food significantly more frequently than adults. In the colony of *C. damarensis* the frequent workers (which are often the juveniles) carry significantly more frequently than infrequent workers (Bennett 1990), while in *Heterocephalus glaber* there is a significant negative correlation between body mass and carrying food (Jarvis 1991; Lacey and Sherman 1991).

Interactive behaviours

Naso-anal interaction

Naso-anal associations, or mutual smelling of the partner's anal region, has not been recorded in *C. damarensis* and together with urino-genital sniffing illustrates that *Cryptomys damarensis* and *C. hottentotus* are behaviourally distinct.

In *C. hottentotus* there was a highly significant tendency for juveniles to initiate naso-anal interactions. The reproductive pair were involved in only 4 % of the interactions, whilst the juveniles were involved in 80 % of the interactions. Juvenile-juvenile interactions constituted 59.5 % of the observed naso-anal associations.

By contrast in *H. glaber*, the majority of naso-anal interactions occur between the reproductive animals. High ranking non-reproductive colony members are less frequently involved and juveniles rarely or never (Jarvis 1981, 1991; Lacey et al. 1991). In *H. glaber*, the behaviour is primarily important in the pair-bonding between the reproductives and they rest in this position in the nest (Jarvis 1991). In *C. hottentotus* the function of the behaviour is not apparent, but it may be important in maintaining colony cohesion.

Urino-genital sniffing

Urino-genital sniffing was observed in *C. hottentotus*, and occurred away from the nest. Although the behaviour was unrelated to gender or age, the reproductive pair tended to receive few of these behaviours in comparison to the more subordinate individuals. The function of urino-genital sniffing is unknown. It may possibly serve to identify individuals as belonging to the colony or to determine which of the two interacting animals is dominant.

Sparring

In all species of the Bathyergidae sparring appears to play an important but yet undefined role in the development of the pups. In both solitary and social genera it begins early in the life of the pup. In *Cryptomys*, sparring begins about 10 days after birth (Bennett and Jarvis 1988a; Bennett 1990), while *H. glaber* pups begin to spar when 14–20 days old (Jarvis pers. comm.). The solitary *Bathyergus suillus* and *Bathyergus janetta* begin to spar 13 and 16 days after birth (Jarvis, pers. comm.), while *Georychus capensis* begins later (35 days) (Bennett and Jarvis 1988b).

In all the solitary genera, sparring is between litter mates and the intensity increases until injury is inflicted or the pups disperse. It is also possible that in the young mole-rats the increased frequency of sparring is a consequence of play, but as the solitary pups develop sparring becomes more intense with escalation into fighting, this does not take place in the social mole-rats. In the social bathyergids, sparring is initially almost entirely between litter mates, though, the older juveniles also spar with adults. The adults appear tolerant to the young mole-rats and allow the juveniles to spar with them very vigorously. The reproductive animals in the genus *Cryptomys* spar throughout their lives. Thus the reproductive male and female *C. hottentotus* spar predominantly among themselves and rarely with the other adults. The reproductive male *C. damarensis* rarely sparred. The reproductive female was involved in many interactions but these were mostly with young animals (Bennett 1990). Injuries were not inflicted during any of the encounters observed. The frequent worker caste in *C. damarensis* contains many of the "younger" animals within the colony which could explain the tendency for frequent workers to spar more readily than infrequent workers. Sparring interactions in *H. glaber* (called tooth fencing and incisor tussels) continue until the animals are about 2 years old then become infrequent.

The significance of sparring in the social bathyergids is at present open to conjecture. Two possible roles are, firstly, a training for defence of the colony and secondly establishing a position within the colony hierarchy.

In both *C. hottentotus* (this study) and *C. damarensis* (Bennett 1990) there is a strong positive correlation between the frequency with which an animal initiates sparring and allogrooming ($r_s = +0.7$ and $r_s = +0.5$ respectively). This perhaps suggests that both behaviours play a role in establishing a young animal within the colony hierarchy. In

sparring the juveniles interact most with the reproductive pair and with other juveniles, while in allogrooming the juveniles interact with the reproductive male.

Within the Geomyidae, Spalacidae and Ctenomyidae, sparring interactions are not reported to occur amongst either the young or adults, but adult spalacids placed together do fight (ANDERSEN 1978; PEARSON 1959; NEVO 1961, 1969).

Tail-Pulling

Tail-pulling occurs in the social mole-rats *Heterocephalus* and *Cryptomys*. The behaviour occurs during cooperative burrowing (JARVIS 1969; BENNETT 1988). The act of tail-pulling in the genus *Cryptomys* appears to be associated with the dominance of particular individuals, the dominant mole-rats pulling the tails of the subordinate mole-rats. In *C. hottentotus*, of the eight occasions on which tail pulling was observed, seven involved the dominant animals pulling the tails of subordinates. In the Damaraland mole-rat, "frequent workers" used tail-pulling significantly more frequently than infrequent workers (BENNETT 1990). Tail-pulling in *C. damarensis* is employed mainly during chain digging sequences. In such a sequence three mole-rats may be burrowing in a particular sector of the burrow. However, after a period of time one of the posteriorly directed mole-rats may pull the tail of an anteriorly positioned animal in an attempt to exchange digging positions. Tail-pulling may also be used to remove an individual resting or blocking a particular entrance or sector of the burrow.

Allogrooming

In *C. hottentotus*, juveniles bodily allogroom significantly more frequently than adults. The juveniles groomed other juveniles and the reproductive male in preference to other colony members.

In a colony of *C. damarensis* containing two litters of known age animals (BENNETT 1990) allogrooming by the reproductive male was directed towards the reproductive female. The reproductive female most frequently allogroomed the reproductive male and her most recent litter (hereafter called juveniles). All age groups also groomed the juveniles, while the juveniles themselves groomed the reproductive pair, the most dominant non-reproductive male and a female yearling. The reproductive male was groomed by all of these age and sex categories of young colony members while the reproductive female was only groomed by her most recent pups and the reproductive male.

Ano-genital allogrooming in *C. hottentotus* differed from more generalised allogrooming in that it almost always involved juvenile animals. All the other colony members (excluding the reproductive male) ano-genital groomed the juveniles.

The juveniles directed much of their ano-genital allogrooming towards the adult female colony members (in particular the reproductive female) as well as between the juveniles themselves. Ano-genital allogrooming between adult animals was uncommon.

Allogrooming in the genus *Cryptomys* could serve two main roles, to remove external parasites or as an appeasement behaviour.

Information concerning external parasites associated with *C. damarensis* and *C. hottentotus* is meagre (SHORTRIDGE 1934; DE GRAAFF 1972). Small mites are found in the pelage of the common mole-rat *C. hottentotus* (BENNETT, unpubl.).

Allogrooming results in close physical contact between individuals and its performance could therefore have an indirect appeasement action. This interpretation is supported by the fact that the colony members in general tend to groom the dominant reproductive mole-rats (BENNETT 1988). This has certainly been suggested for social mongooses (RASA 1977). The dwarf mongoose (*Helogale undulata rufula*) occurs in small colonies with a strict monogamous breeding set up. A high degree of division of labour exists within the group which is not unlike that of *C. damarensis*. In such groups there are definite

preferences for subordinate mongooses to groom the dominant animal of the opposite sex (Rasa 1977). Social grooming also occurs in the common marmoset *Callithrix jacchus* in which subordinates groom their peers, the reproductive pair (Rothe 1971; Abbott 1984). Kinloch (1982), observed allogrooming in groups of *C. hottentotus* resting in the nest areas, however, quantitative studies on the frequencies of allogrooming were not reported. In the naked mole-rat, allogrooming is not apparent between colony members, perhaps because they lack a pelage (J. U. M. Jarvis, pers. comm.).

Autobehaviours

Autogrooming

In the *C. hottentotus* colony, no tendency occurred for juveniles to autogroom more frequently than adults. However, in *C. damarensis*, juveniles tended to autogroom more frequently than adult animals (Bennett 1990).

In *Cryptomys*, juvenile animals tend to autogroom significantly less frequently than they allogroom (Binomial Test $p = < 0.05$ probability rejection level).

The problem of maintaining a clean coat is exacerbated by living a totally subterranean existence. Burrowing and digging movements through the soil result in sand and soil particles being dislodged and caught within the fur. The pelage is kept clean by regular and thorough grooming and also by shaking of the fur and twitching of skin. In *C. hottentotus*, there was no correlation found betweeen the frequency of excavating and autogrooming ($rs = +0.23$). There was, however, a significant correlation between the frequency of moving soil or sawdust and that of autogrooming ($rs = +0.77$). Similarly, in *C. damarensis* there was no correlation between the frequency of excavating and that of autogrooming (Bennett 1990). However, in contrast to *C. hottentotus* there was no correlation between the frequency of moving sawdust and that of autogrooming (Bennett 1990). Grooming sequences within the rodent moles are very similar. Grooming begins with the face, the slightly cupped paws are used independently as they are rubbed over the incisors, nasal region and the cranial area. The incisors and forefeet are used synergistically to groom the abdomen, genitalia and the parts of the hind region which are accessible. The digits are cleaned using the incisors. The above description is common to *Tachyoryctes splendens, Heliophobius argenteocinereus, C. damarensis, C. hottentotus, G. capensis* and *H. glaber* (Jarvis 1969; N. C. Bennett, pers. obs.).

Autogrooming in the genera *Cryptomys* and *Georychus* appears to mainly occur after awakening from a period of rest, after a visit to the toilet area or after a period of soil movement. The behaviour pattern occurs similarly in *T. splendens* and *H. argenteocinereus* (Jarvis 1969), but in *H. glaber* occurs almost exclusively, in the toilet area, prior to, during and after urination and defaecation.

Tooth-sharpening

Tooth-sharpening is seen in all the bathyergids (Jarvis 1969; N. C. Bennett, pers. obs.). The tooth-sharpening behaviour is essentially the same in all the mole-rats and takes place when the animal is drowsy and usually preceeds "sleep".

In *C. hottentotus*, there was no animal which tooth-sharpened more than another. However, after recruitment had occurred in a *C. damarensis* colony "frequent workers" sharpened their teeth significantly more than "infrequent workers" (Bennett 1988). These frequent workers were the two recent litters and a small adult animal. It is possible that the frequent workers, the animals that do most digging, had a greater rate of incisor growth compared to the rest of the colony or that their activities were blunting their incisors.

Brett (1986) noted that when *H. glaber* dug through very hard soil they had to make frequent stops to sharpen their incisors.

Coprophagy

Autocoprophagy occurs in all the southern African bathyergids (*C. hottentotus*: Kinloch 1982; *G. capensis*: Bennett, pers. obs.; *B. suillus*: J. U. M. Jarvis, pers. comm.). Coprophagy is undertaken to enhance the digestion and absorption of food, (particularly of cellulose) which do not readily yield their nutrients. The available literature on the subterranean rodent families Geomyidae, Ctenomyidae and Spalacidae make no mention of these rodents practising coprophagy.

To my knowledge allocoprophagy, involving pups and other colony members, is unique to the social Bathyergidae. Allocoprophagy includes both begging faecal material directly from the anus of a conspecific and the consumption of a voided pellet, picked up in the toilet area.

Coprophagy is commonly undertaken in *H. glaber* (Jarvis 1981); weaning pups beg faeces from other colony members, begging for them with mewing cries and tugs of the donor's anus. When very gravid, the breeding female of *H. glaber* has difficulty in doubling up to reach her anus. She begs faeces from other adults and subadults engaged in autocoprophagy in the nest area (Jarvis 1991). Unlike the gravid *H. glaber*, pregnant reproductive cryptomyids do not appear to beg faeces from other colony members. However, the pups of *C. hottentotus* and *C. damarensis* beg faeces from their mothers after weaning. Allocoprophagy at this age may allow the transmission of valuable gut fauna from the parent to the offspring, as well as providing the weaning pups with easily assimilable food.

Toilet behaviour

The exact function of grooming in the toilet area and the subsequent smearing of a fluid on exit from this region is unknown. It appears to occur mainly within the social bathyergids (Jarvis 1981).

The marking agent may serve as an indicator in the same way as urination within the burrow is believed to act as an orientation marker (Kinloch 1982). The marking of the section of the burrow leading away from the toilet area and the actual entrance may well act as a cue for orientation within the particular region of the burrow system. The frequency of marking may well inform each animal of the degree of use of this part of the system.

Smear marking may familiarise each mole-rat with the odour of other colony members. This would allow members of the colony to differentiate between conspecifics and intruding individuals. Marking could be of importance in expressing the internal sexual status of each animal, the urine merely reflecting the corresponding plasma hormone concentration, in this respect the reproductive pair of *C. hottentotus* were found to smear mark significantly more frequently than non-reproductive colony members. In contrast there was no significant tendency for any one animal to urinate any more frequently than another. The second focal area in the burrow system which receives frequent visits and could be involved as a site of the release of a chemical which initiates suppression of reproduction in the females other than the reproductive females, is the toilet area. Mole-rats entering the communal toilet area not only urinate and defecate in this area but also smear mark and groom. This area, as well as the nest therefore exposes colony members to each others' semiochemical signals and will serve to inform each other of the sexual status of colony members and impart a general group odour. If reproductive suppression of colony members by the reproductive female has a chemical component, then the toilet area would be an opportune site in which to effect this control. It is possible that chemicals,

such as volatile hormones or pheromones, are released at the toilet areas in the urine by the reproductive female.

The advantages of having colonies in which reproduction is limited to a single female seem to mainly relate to inclusive fitness and the associated benefits of altruistic behaviour (Rasa 1977). For example food sharing, an altruistic behaviour is exhibited by the colony, despite the unequal involvement of the colony members in the various burrow maintenance activities. This is a strong indication of differential participation in burrowing and food harvesting occurring in the natural environment. *Cryptomys hottentotus* colonies involve a reduction in individual reproduction to an extent that only one female in the colony is reproductive. This offers some of the strongest evidence for the phenomenon of kin selection.

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Zusammenfassung

Aspekte des Sozialverhaltens einer in Gefangenschaft gehaltenen Kolonie des südafrikanischen Graumulls Cryptomys hottentotus

Das Verhalten von Graumullen *(Cryptomys hottentotus)* in einer Laborkolonie wurde qualitativ und quantitativ untersucht. Die Kolonie bestand aus einer reproduktiven und einer nichtreproduktiven Kaste. Die nichtreproduktiven Tiere ließen sich in „Arbeiter" und „Gelegenheitsarbeiter" einteilen. Das Ausmaß der geleisteten Arbeit stand in keinem direkten Verhältnis zur Körpermasse der Tiere.

Die beobachteten Verhaltensweisen ließen sich drei Hauptkomplexen zuordnen: Bauinstandhaltung, Interaktionen und Individualverhalten. Bei der Analyse sozialer Interaktionen wurden Alter und Klassenzugehörigkeit berücksichtigt. Arbeitergruppen unterschieden sich in ihrer Grabaktivität nicht signifikant von anderen. Jungtiere trugen häufiger Nahrung ein als Adulte.

Eine positive Korrelation zwischen den Verhaltensweisen des Initiators und denen des Empfängers wurde in folgenden Fällen festgestellt: gegenseitige Genitalpflege; Kampfspiel; naso-anale Kontakte und Beschnuppern des Urogenitalbereichs. Das reproduktive Paar pflegte sich nur gegenseitig. Gegenseitige Fell- und Genitalpflege, naso-anale Kontakte sowie Kampfspiele traten bei Jungtieren häufiger auf als bei Adulten. Viele der Verhaltensweisen scheinen eher vom Alter abhängig zu sein als von der Klassenzugehörigkeit.

In der Kolonie gab es einen abgegrenzten Toilettenbereich, in dem reproduktive Tiere signifikant häufiger markierten als andere Koloniemitglieder.

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WISSENSCHAFTLICHE KURZMITTEILUNGEN

Food habits of the Lesser false vampire, *Megaderma spasma*, from Kuala Lompat, Peninsular Malaysia

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Very little is known of the feeding habits of Malaysian microchiropterans except for some detailed studies on *Hipposideros pomona* (Zubaid 1988a), *Hipposideros armiger* (Zubaid 1988b) and *Taphozous melanopogon* (Zubaid 1990). The main problem with the study of microchiropteran feeding habits is that bats thoroughly chew their food, making identification of most prey remains below the family level practically impossible and thus giving only an indication of the order of importance of the dominant prey items (Whitaker 1988). However, the study of microchiropteran feeding habits is important as bats are thought to play an important role in influencing insect populations both in forests and cultivated lands (Hill and Smith 1984; Coulson and Witter 1984; Benjamini 1987).

This study was carried out at Kuala Lompat, Krau Game Reserve, Pahang, at a permanent day-time and feeding roost of between two and five *Megaderma spasma*. The roost was located under the asbestos roof of an abandoned room in an old wooden rest-house. This was sited in a grass clearing with fruit trees, bordered on one side by the 500 km^2 lowland dipterocarp rainforest of the Krau Game Reserve, and on the other by a small river and extensive mature rubber estates.

All observed food discards were collected from beneath the roost, at irregular intervals from March 1988 to September 1990. No attempt was made to determine prey selection versus prey availability as the remains were collected in conjunction with another study.

The table lists the food material collected. The samples from the various months were pooled due to small sample sizes (n = 1632). The remains were compared with identified collections in the

Estimated proportions of animal remains collected from the roost of *Megaderma spasma*

Food item	Proportion (%)
ORTHOPTERA	
Tettigonidae	51.5
Blattidae	12.5
Acrididae	2.0
Phasmantidae	2.0
Gryllidae	3.0
Mantidae	1.0
COLEOPTERA	
Scarabaeidae	12.0
LEPIDOPTERA	
Satyridae	3.0
Amathuacidae	1.0
Danaidae	1.0
Geometridae	0.5
Papilionidae	0.5
Arctidae	0.5
Nymphalidae	2.0
Noctuidae	1.5
HYMENOPTERA	
Formicidae	0.5
ISOPTERA	4.0
HOMOPTERA	0.5
Cicadidae	0.5
ODONATA	0.5
ANURA	
Rhacophorus appendiculatus	0.5

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Zoology Museum, University Kebangsaan Malaysia. The proportions are percentages of the total collected remains and the procedure used followed that of LaVal and LaVal (1980). The majority of the remains were wings and wing-cases, with a few legs. These had evidently been dropped whilst the head, thorax and abdomen of all prey were fully consumed. Most of the remains were of big insects found typically on foliage. This, and the presence of a tree-frog, imply that most prey were probably picked from the vegetation. Orthopterans and coleopterans made up a large proportion of the diet, 72.5 % and 12 % respectively. Only one vertebrate, the frog (only the legs remained), was recovered from the roost site.

Amongst the lepidopteran remains (12 %), there were equal proportions from typically diurnal and typically nocturnal families. This again may be evidence that food is picked from vegetation, rather than caught while the prey is in flight.

There is no previous detailed information concerning the food habits of *M. spasma*. Medway (1982) and Payne et al. (1985) only mention that this species eats "large insects" and "small vertebrates" (including other bats) but did not mention the specific types of prey that are consumed. The results of this study indicate that *M. spasma* feeds selectively on orthopterans (Table) which make up approximately three-quarters of the diet followed by coleopterans. Although this species is known to eat other small vertebrates, the findings in this study indicate that they are a minor component of the diet.

Brosset (1962) noted that *M. spasma* hunts near its daytime roost and tends to return to its roost to consume the prey. If this is also true of the species in Malaysia, then the results of the dietary analysis could be considered to be a reasonably accurate reflection of its feeding habits.

Most orthopterans are phytophagous while the coleopterans are considered to be among the most destructive insect pests of forest trees (Coulson and Witter 1984). Birds, bats and other small mammals are among the most significant vertebrate predators of insects (Coulson and Witter 1984; Speight and Wainhouse 1989) but quantitative studies concerning bats are lacking. Although *M. spasma* occurs only in small groups, not in big roosts (Brosset 1962; Medway 1982), and takes only a limited range of insect prey (this study), it is likely that the cumulative effect of Peninsular Malaysia's rainforest bat species (Medway 1982), each with it's own dietary range (Zubaid 1988a, 1988b, 1990; this study) has a significant influence on the low-density dispersed populations of rainforest insects (Elton 1973).

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Distribution and local range of the Orinoco dolphin (*Inia geoffrensis*) in the Rio Apure, Venezuela

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Orinoco dolphins (*Inia geoffrensis*), in Venezuela known as Toninas, occur in the Orinoco, Rio Negro and tributaries in Venezuela. We intended to investigate: 1. Whether *Inia* is solitary and grouping is a result of aggregation in favourable habitats; 2. Whether there is evidence for migration, possibly in connection with seasonal movements of fish (Lowe-McConnell 1964); 3. Whether *Inia* is territorial.

We carried out a 17 day survey by boat during the end of the rainy season in 1989. Between July 27th and 30th, we covered 45 km of the Apure river to the west of San Fernando de Apure, using a 4.5 m long engine powered aluminium canoe. Between August 5th and 15th we covered 156 km of the Apure to the east of the town, 27 km of the Orinoco upstream from the mouth of the Apure and 27 km of the Apurito upstream from its mouth into the Orinoco using a 10 m long engine powered wooden dugout-canoe. Hours of observations were between 8:30 and 17:30 every day. Irregular rainfall interrupted the work so observation times could not be further standardized. Cloud cover and height of ripples on the water surface were noted on a scale from 0 (slight) to 3 (severe). The distance covered was followed on a map and sightings noted every 3 km interval. Numbers of sightings per interval were compared to a Poisson distribution of equal mean, using the chi square test (for methods refer to Magnusson et al. 1978).

For each sighting, depth of the river and stream velocity were noted: The depth was found by lowering a 5 kg iron weight attached to a rope with knots at 50 cm intervals to the bottom of the river. Stream velocity was measured holding the boat steady against the current with reference to a landmark on shore. A nail attached to a rope was lowered into the water up to a marked point. The rope was attached above a scale over which it swept as the current displaced the nail, giving a relative estimate of stream velocity. Measurements of depth and current speed were compared to the size of sighted groups, using Spearman's rank correlation coefficient (r_s).

The study was complemented by observations by boat and from shore of dolphins within a 3.5 km long stretch of the Apure. These observations were carried out from 22nd–26th August between 6:00 and 18:00 hours. The position of the animals was plotted on a large scale map. Natural markings of individual dolphins helped in this tracking effort.

The average density of *Inia* surveyed between August 5th and 15th was 0.56 animals per km with an average sighting frequency of 3.91 animals per hour. Highest densities were encountered in the Apurito (1.15 animals per km, 8.6 sightings per hour). Current and turbulence lead to inconsistency in boat speed, affecting the values for sightings per unit effort.

Individual *Inia* were found to be patchily distributed. The distribution of groups did not differ significantly from the Poisson distribution (Table). 58 % of our sightings were groups of two or more (Figure).

There was a significant (Spearman's rank coefficient $r_s = -0.608$; $P < 0.01$) relationship between group size and stream velocity. Most large groups were encountered in slow

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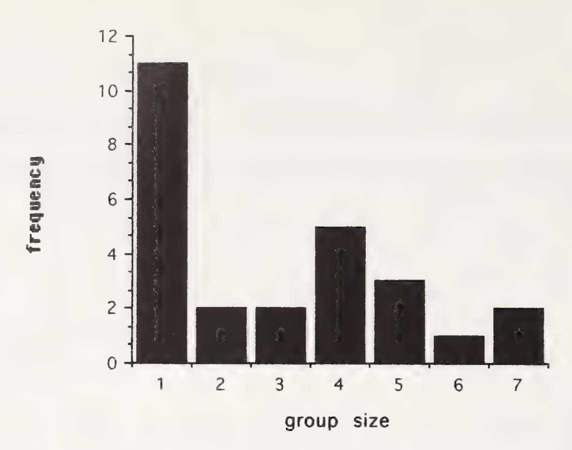


Fig. 1. Frequency distribution of *Inia geoffrensis*

running sections of the river, vicinity of flooded banks or clearwater tributaries. Most of the sightings occurred in 10 to 12 m deep water within 50 m from the bank.

During the observations following the boat survey, most groups of *Inia* were encountered regularly within defined ranges of approximately 130–800 m along the river. Dolphins following the boat repeatedly remained behind at fixed points but ranges overlapped and interactions between neighbouring groups occurred. No aggressive interactions were observed.

58 % of our sightings represent groups of two or more individuals compared with 20 % in the study of Magnusson et al. (1980). In accordance with points 1. and 2. of the introductory remarks, possible reasons could be:

1. Seasonal migration: *Inia* has been reported by Trebbau and van Bree (1974) to enter floodplains and smaller tributaries during the rainy season, though Best and Da Silva (1986) do not recognize any seasonal trend in the data, possibly due to lower annual

Distribution of individuals and groups per 3 km interval for each section of the survey as indicated above the columns

Statistical results	Apure (201 km)	West of San Fernando (45 km)	East of San Fernando (156 km)	Orinoco	Apurito
Individuals					
n	67	15	52	9	9
$\bar{x}$	0.43	0.27	0.48	1.11	3.44
Σx	29	4	25	10	31
Σx^2	119	6	113	34	213
Variance	1.61	0.35	1.98	4.86	13.20
$\chi^2 = \Sigma(x-\bar{x})^2/\bar{x}$	247***	18.25 NS	210***	20.61**	31.45***
Groups					
$\bar{x}$	0.194	0.200	0.308	0.556	0.667
Σx	13	3	16	6	6
Σx^2	19	3	16	8	8
Variance	0.250	0.171	0.217	0.280	0.500
$\chi^2 = \Sigma(x-\bar{x})^2/\bar{x}$	84.936*	12.000 NS	36.000 NS	14.789 NS	6.000 NS

The number of intervals in a section is noted as n and average sightings per interval as $\bar{x}$. Significant values for chi squared are marked * for $P < 0.05$, ** for $P < 0.01$ and *** for $P < 0.001$. For these, if the mean is maller than the variance, the distribution is patchy.

fluctuations in rainfall further south. The tendency of *Inia* to aggregate may be related to movements of characids and catfish into the floodplains to spawn and feed (LOWE-MCCONNELL 1964, 1975). In the floodplains and the Apurito high densities of young catfish could be observed skimming the surface. In the fast flowing Apure, young catfish were occasionally observed in direct vicinity to the bank (maximum 3 m away).

2. Opportunistic aggregation: Several authors (BEST and DA SILVA 1986; GEWALT 1978; TREBBAU and VAN BREE 1974; TREBBAU 1975) have reported that the animals aggregate around anchored boats, areas of turbulence and in the mouths of tributaries. DA SILVA (pers. com.) suggests that aggregations are not permanent as the animals may segregate after short periods. During our observations single animals and groups were frequently joined by others and would then separate. Our observations therefore lead to the same conclusion.

Earlier studies suggest that *Inia* may be a sedentary species occupying localized ranges at least during part of the year (see BEST and DA SILVA 1986, for a review). Similar observations lead TREBBAU and VAN BREE (1974) to suggest that *Inia* may be territorial. Our observations of resident groups and individuals indicated that *Inia* occupies a limited range for at least part of the year. However, we found no evidence for aggressive or avoidance behaviour. We would therefore support BEST and DA SILVA's (1986) conclusion that *Inia* occupies an undefended homerange.

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Reproductive behaviour and development of the young of the chacoan peccary (*Catagonus wagneri* Rusconi, 1930) in the Paraguayan Chaco

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Herein, anecdotal information on Taguá reproduction and development is described; findings are compared to reproduction and development of other Tayassuidae species where information is available. The study facility (Proyecto Taguá), located in the Central Paraguayan Chaco, has been described in detail elsewhere (i.e., Handen and Benirschke 1991; Kingswood and Brooks 1991), and is part of the natural range of Taguá, as wild specimens (two adults and a three month old infant) were sighted on the estancia where the study site was located. Semi-captive Taguá were studied for a year (September 1989 to August 1990); study times varied between 0530–2000 hours, though most of the study durations were from 1400–1800 hours. Observations were made from one of two high-seat blinds, and complemented by random observations on foot.

Copulation occurred among adults (male = M1, female = F1) on November 1, 1989, at 1510 hours, with a temperature of 34 °C. Actual conception remained unconfirmed, but F1 gave birth 184 days later. Two days after this copulation (1210 hours, 34 °C), M1 was observed following F1 next to a tajamar (temporary, manmade pond), exhibiting pre-copulatory behavior. Another male (who was dominant over M1) approached M1 and F1 with his dorsal hair halfway erected. M1 then declined, and the pair exhibited what was probably a submissive behaviour, rooting in tajamar mud, side by side. Then shortly thereafter, M1 sniffed the ano-genital region of another Taguá which proceeded with a head-slice movement against M1. F1 exhibited precopulatory behaviour with an alternate male while in the presence of M1; immediately afterwhich, F1 exhibited precopulatory behaviour with M1. M1 also exhibited precopulation and air-mounting with an alternate female. From these observations, it seems likely that promiscuity was present in both sexes. Due to hierarchial rank or inhibition by the female, some males were unable to proceed with precopulatory behavior. Social order between sexes in Taguá appears to be complex, and remains largely unknown. Precopulatory behavior was observed most frequently from May 9 to June 8, between the hours of 0730–1600, with temperature varying between 16 °C–30 °C.

The earliest recorded age-specific fertility at Proyecto Taguá was a litter of three at a maternal age of 21 months (n = 1). Mayer and Brandt (1982) estimated the youngest pregnant Taguá sow (n = 1) in their study to be 13–18 months of age. Comparatively, the youngest collared peccary sows (n = 2) in Sowls (1966) study gave birth at 13.5 months. White-lipped peccary sows become sexually mature at 18 months (Eisenberg 1989). Litter sizes at Proyecto Taguá ranged from 1 to 4 (N = 9; SD = 1.1; mode = 3); whether or not infanticide occurred is unknown. The findings of Mayer and Brandt (1982) are similar; the average litter size at Proyecto Taguá was 2.33, whereas Mayer and Brandt (1982) had an average of 2.46 (N = 10; r = 1–4; mode = 2–3) for neonatal litters sighted live in the field. Additionally, a mean litter size of 2.17 (N = 29; r = 1–4; mode = 2) was obtained in collared

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peccaries (SOWLS 1966). MAYER and BRANDT (1982) reported 2 fetuses from a pregnant white-lipped peccary sow (N = 1) collected in the Paraguayan Chaco, and indicated that litters of 3 were rare. FRÄDRICH (1972) reported that 9 of 10 white-lipped peccary litters at the Berlin Zoo consisted of twins.

Data were collected daily for specific individuals of the 21 young born at Proyecto Taguá as of August 9, 1990. Learning processes are summarized hereafter (mean age [days] with range [r] when a particular learning process was first observed for n individuals appears parenthetically at the end of each account) as follows: Feeding: mouthing food or maneuvering with nose, but not eating (n = 4; mean = 4.0; r = 2–6); nibbled or chewed food, but no consumption (n = 3; mean = 13.5; r = 13–15); rubbed at top layer of soil with snout (n = 1; mean = 14.0); ate solid food for first time (n = 4; mean = 18.0; r = 17–19); maneuvering food with foot and mouth (n = 4; mean = 26.5; r = 14–39). Litter cohesion: litter of three came to feeding area together for first time (n = 2; mean = 6.0; r = 4–8). Survivorship skills: Taking cover on ground, or behind adult when warning stimulus is elicited (n = 3; mean = 5.1; r = 5–6); eliciting warning stimulus (n = 1; mean = 54.0). Intraspecific competition: individual pushes a younger nursing infant, in order to nurse (n = 2; mean = 13.5; r = 8–19); average proportion of days younger infant was than competitor (n = 2; mean = 0.7; r = 0.6–0.8). Playing: infants play fighting (n = 2; mean = 23.5; r = 22–25). Independence: arriving at feediung area alone, with infants, or staying behind after others left (n = 6; mean = 192.5; r = 70–248).

The infants were able to run within a couple of hours after birth. The pelage was not completely dry prior to first quadrupedal movement. Nursing was done from the side, from the rear, standing up, kneeling on front knees, sitting, or kneeling on all four legs. Standing up from the side was the most frequent position. It was common for infants and older juveniles to nurture infants, much as the adults did. Nurturing Taguá were not always related to the nurtured individual, suggesting that Taguá maintain strong inter-familial group cohesion.

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Barquez, R. M.; Mares, M. A.; Ojeda, R. A.: **Mammals of Tucuman – Mamiferos de Tucuman.** Norman: Oklahoma Museum of Natural History 1991. Illustrated by N. Giannini. 282 pp. US $ 17.00. (Obtainable from the Oklahoma Museum of Natural History, Norman, Oklahoma 73019, USA)

This is a bilingual guide to 95 species of mammals known to occur in Tucuman, a small province which covers only 0.8 % of the territory of Argentina. Nevertheless its fauna is surprisingly rich due to topographic diversity with a number of high-altitude habitats in the Andes as well as subtropical forest and Chacoan thorn scrub in the lowlands.

A key to the orders, families and species is provided which is principally based on external features and measurements which should permit the identification of living animals. However, the authors correctly warn the reader that many small mammals such as rodents and bats are difficult to identify in the hand.

For each species the scientific and common names in English and Spanish are given on a left page, followed by a short description and notes on distribution. Sometimes comments on abundance, habitat or reproduction are added. On the opposite right page rough distribution map, a drawing of the animal and two aspects of the skull are to be found. 10 references of books suggested for further reading and an index to species conclude the book.

The bilingual concept of the guide is promising and should be taken as a model for other local faunas. Without doubt it will help to raise interest in the study and conservation of South American mammals. However, interested laypeople as well as professional users will soon reach the point where they wish to consult a more detailed book or an expert. For example, not a single word indicates why *Thylamys elegans* is used as scientific name for a mouse opossum known as *Marmosa elegans* for long, and the same applies to the rather unusual use of *Pseudalopex* instead of *Dusicyon*. A comment and a reference would have been helpful for readers without access to a mammal library. Also, a scale for each skull and a proportional reduction of the illustrations, at least within one genus, would have facilitated the identification, aspects to be considered in a future edition. The present book convers a nearly blank page of South American mammalogy and just for this reason it is a must for readers interested in neotropical mammals. R. Hutterer, Bonn

Herrmann, M.: **Säugetiere im Saarland.** Verbreitung, Gefährdung, Schutz. Schriftenreihe des Naturschutzbundes Saarland e.V. (DBV). Ottweiler: Michel Verlag 1991. 166 S., 19 Verbreitungskarten, 31 Abb. ISBN 3-923755-25-2

Das Anfang 1991 fertiggestellte Buch ist ein erster begrüßenswerter Versuch, die heute im Saarland lebenden Säugetierarten zu erfassen (ausgenommen die Fledermäuse), was flächendeckend allerdings nicht möglich war. Die Angaben zum Vorkommen und zur Verbreitung der verschiedenen Spezies gründen im wesentlichen auf Beobachtungen und Hinweisen von 156 namentlich genannten „fachkundigen Informanten", die dem Kreis von Förstern, Biologen, Jägern und im Naturschutz engagierten Personen angehörten. Wie der Untertitel des Buches verrät, gelten die Bemühungen des Autors aber nicht nur der Klärung von Verbreitungsfragen; sein Engagement ist mindestens ebenso groß, wenn es gilt, auf die Gefahrenquellen aufmerksam zu machen, denen die Säugetiere in der heutigen Kulturlandschaft ausgesetzt sind; und wie diesen Gefahren begegnet werden kann. Den einleitenden Angaben zur methodischen Seite der Erhebungen schließt sich der Hauptteil des Buches an: Die Auflistung der saarländischen Säugetiere mit Erwähnung auch der inzwischen ausgestorbenen Arten. Den Anmerkungen zur „Biologie" der jeweiligen Art folgen Hinweise zum Vorkommen mit punktueller Verbreitungskarte auf Meßtischblattbasis und Erörterungen zu „Gefährdung und Schutz" der Spezies. Auch zum Thema Wiederansiedlung (Biber, Bär, Elch, Fischotter, Luchs und Wolf) und Faunenverfälschung (Damhirsch, Nutria, Waschbär) wird Stellung genommen. Die Säugetierfauna des südwestlichen Bundeslandes umfaßt (ohne Fledermäuse) 37 Arten einschließlich der Schabrackenspitzmaus. Bislang nicht sicher belegt sind die Sumpfspitzmaus, die Gartenspitzmaus und die Kurzohrmaus; für die Feldspitzmaus fehlen neuere Hinweise, ebenso für den Hamster und die Hausratte. Im Saarland noch nicht aufgetaucht ist offensichtlich der Marderhund, dessen fachliche Benennung *Nyctereutes procyonoides* lautet (nicht *N. procyonides*). Den letzten Teil des Buches widmet der Autor eingehend dem Problem der Gefährdung von Säugetieren durch Umwelteinflüsse. Es werden zahlreiche Gefahrenquellen aufgelistet (Gewässerverschmutzung, Flurbereinigung, Trokkenlegungen, Pestizide, Schwermetalle, Chlorkohlenwasserstoffe, Dioxine, Straßenverkehr usw.), die im Grunde genommen nicht nur für die Säugetiere, sondern für die Tierwelt schlechthin eine Bedrohung darstellen. Im Anhang 1 wird die naturschutzrechtliche Stellung der Arten erläutert, Anhang 2 enthält informative Tabellen mit Ergebnissen von Gewöllanalysen, Anhang 3 schließlich die Namen der Mitarbeiter und Beobachter. Am Schluß findet sich ein umfangreiches Literaturverzeich-

nis, das eigentlich die Auffassung des Autors widerlegt, die Säugetierforschung stecke im Vergleich mit der Ornithologie „noch in den Kinderschuhen". So begrüßenswert das große Engagement des Autors bezüglich des Säugetierschutzes auch ist und so wichtig das von ihm initiierte Vorhaben für die Säugetierfaunistik auch sein mag, so muß man bei alledem auch der deutschen Sprache gerecht werden, auch oder gerade dann, wenn die anzusprechende Zielgruppe Naturschützer und wissenschaftlich interessierte Laien sind. Es würde den Rahmen dieser Rezension sprengen, wollte man all die Wortneuschöpfungen und Satzungetüme, die lapidaren Feststellungen und unbeholfenen Formulierungen aufzählen, die einer strengen redaktionellen Bearbeitung eigentlich hätten zum Opfer fallen müssen. Und so findet sich ein „undokumentierter Bestandsrückgang" (S. 77) neben einer „Feindvermeidungsstrategie" (S. 51), der „generalistische Beutegreifer" (S. 52) neben „leerstehenden Habitaten" (S. 60), die „bärische Aktivität" neben dem „nomadischen Erschöpfungsjäger" (S. 80), die „Wanderbarriere" (S. 40) neben den „Extrembiotopen" (S. 42) und die „potentiell wichtige Gefährdungsursache" (S. 78) neben dem „Habitatelement" (S. 42). Adulte Erdmäuse nutzen ihre Streifgebiete weitgehend „exklusiv" (S. 50). Der Baummarder kann als „Indikatorart für den Kronenbereich innerhalb des Ökosystems Wald angesehen werden" (S. 85). Beim Rothirsch ist „für die Populationsentwicklung historisch das wiederholte Eintreten von Ausrottungsphasen wesentlich" (S. 109). Sein „Gen-Pool" wird durch künstliche Selektion, die Jagd „verfälscht", derjenige der einheimischen Population „dürfte erloschen sein" (S. 110). Und vom Nutria heißt es, daß er während einer Nacht mehrere Kilometer „Gewässerlauf abstreifen" kann (S. 67). Von den von Zwergmäusen ursprünglich besiedelten Lebensräumen sind „nur noch Bruchstücke" übrig (S. 65). Hausmäuse werden „häufig in Fallen gefangen" (S. 61). Und die Hausratte schließlich hat eine „geringe Ausbreitungsdynamik" (S. 60). Wer sich an solchen oder ähnlichen Formulierungen nicht stört, auch nicht an dem Satz, daß Feldhasen „auch durch Veränderungen der Vegetation hin zu nitriphilen Bedingungen infolge Düngereintrags durch die Landwirtschaft und der Stickoxyde aus der Luft sowie durch Verlust von strukturreichen Lebensräumen infolge der Flurbereinigung" bedroht sind (S. 37), dem kann die Lektüre empfohlen werden. Die Qualität eines Beitrages kann nicht am Inhaltlichen allein, sie muß auch an seiner Form gemessen werden.

H. Reichstein, Kiel

Bayer, Shirley A.; Altman, J.: **Neocortical Development.** New York: Raven Press 1991. 256 pp., 208 figs., 2 tables. US $ 161.50. ISBN 0-88167-778-7

As one of the most important and most complicated parts of the mammalian forebrain the neocortex has been the subject of a variety of scientific investigations with regard to both its structural appearance and functional importance as well as practical applications and theoretical interpretations. Nevertheless, phylogenetic origin, ontogenetic development and evolutionary diversification are the main issues of zoological evaluations. In this sense, the book by Shirley A. Bayer and Joseph Altman fills a certain gap in our knowledge, as it is devoted to the ontogenetic development of this portion of the brain. The authors report on own results very accurately and in detail, mostly obtained from an impressively large and well-defined sampling of material using normal histological and experimental methods (labeling, x-irradiation). However, the one drawback of this descriptive book is that it is based on only one species and a special breed, namely, the laboratory rat of the Wistar strain.

In contrast to the rather misleading title of the book, results are presented on a rather primitive mammal in its domesticated form possessing a lissencephalic and structurally less complex cortex. Furthermore, developmental changes during the postnatal period are not included. Despite these restrictions, there are 17 chapters associated with 4 major sections, of which the first gives a brief historical review and provides overviews of major morphological and histological changes that occur from embryonic day 11 (E11) through birth (E22). Daily changes are recorded qualitatively and quantitatively, and a global "chronoarchitectonic map" is given on the basis of morpho- and neurogenetic gradients of growth and differentiation.

The second section of the book is concerned with the entire embryonic development of the neocortex (neuroepithelium, subplate, cortical plate, cell migration, maturation, stratification). Reflecting on their results the authors hypothesize an early recognition of prospective cell material. According to their theory, only radially cleaving cells in the embryonic ventricular zone differentiate to precursors of neurons, while variably cleaving cells lose their attachment to the ventricular wall and develop into neuroglial and ependymal elements. Further cell proliferation at first results in an early stage of cortex formation consisting of a primordial plexiform layer with cells of the future layers I (marginal layer) and VII (subplate). A second stage is established later, resulting in the formation of the cortical plate (future layers VI–II). This process partitions the primordial layer into superficial and deep parts. Prior to the definitive stratification, a two-tiered construction is postulated, forming a lower tier (VI/V) and an upper tier (IV/III/II). According to neurogenetic development, the neurons in layers VI–II are generated in three spatio-temporal gradients: 1. the radial gradient (older neurons are situated in the depth of the cortex, younger more superficially); 2. the transverse gradient (neurons situated ventrolaterally tend to be older than those situated dorsomedially); 3. the longitudinal gradient (neurons closer to the frontal pole tend to be older than those closer to the occipital pole).

The third main section of the book describes the intrinsic neurogenetic gradients within specific areas (visual, auditory, somatosensory, motor, and limbic cortical). It becomes evident that the general pattern of neurogenetics is modified in some way between various cortical areas, e.g., in the upper tier. Furthermore, primary sensory areas always contain younger neurons than their respective secondary sensory areas. The fourth section of the book includes theoretical issues, a summary, and conclusions. It is followed by appendices with descriptions of the methods applied.

To summarize, most of the results are not new and some theoretical issues seem to overestimate and generalize the results obtained in Wistar rats to a comprehensive phylogenetic interpretation. Nevertheless, this is a well illustrated and excellent compilation of embryonic neocortical development of the rat with some interesting and stimulating interpretations. D. KRUSKA, Kiel

MARTIN, A. R. (Hrsg.): **Das große Bestimmungsbuch der Wale und Delphine.** München: Mosaik Verlag 1991. 192 S., 200 z.T. farbige Abb. DM 49,80. ISBN 3-576-10003-2

In dem vorliegenden, von ANTHONY R. MARTIN herausgegebenen Band sind sowohl die Abbildungen als auch der Text von hoher Qualität. Der Herausgeber, welcher im Vorstand der 'Sea Mammal Research Unit' in Cambridge, England, tätig ist, hat zehn wissenschaftliche Mitarbeiter und zwei Künstler zur Erstellung des Werkes herangezogen. Gemeinsam haben sie einen höchst informativen, harmonischen und sachlich wie auch ästhetisch ansprechenden Band im DIN-A 4-Format gestaltet.

Das Buch ist in zwei Hauptabschnitte gegliedert, einen allgemein biologischen und einen mit den Artbeschreibungen. Der erste Hauptabschnitt behandelt zunächst die Besonderheiten der Wale als marine Säugetiere, dann wird kurz auf ihre Entwicklungsgeschichte eingegangen. Gesonderte kurze Kapitel beschäftigen sich mit dem Schwimmen und Tauchen, mit den Sinnen, der Intelligenz, der Nahrungsaufnahme, dem Sozialverhalten der *Cetacea* und ihrer Ontogenese sowie mit ihren Lebenszyklen. In den abschließenden Kapiteln des ersten Hauptabschnittes werden Strandungen, Walbeobachtungen und Walforschungen sowie der Einfluß der Fischerei und der Meeresverschmutzung auf die Meeressäuger besprochen.

Der zweite Hauptabschnitt des Buches behandelt 11 Bartenwal- und 67 Zahnwal-Arten. Jede Artbesprechung ist farbig illustriert, meist mit ausgezeichneten Photos. Die Größe jeder Art wird dadurch anschaulich gemacht, daß ihr Umriß proportionsgerecht neben den eines Tauchers gesetzt wird. Die Beschreibung jeder Walart bietet klar gegliedert folgende Einzelheiten: 1. Systematik; 2. die populären Bezeichnungen der Art; 3. Beschreibungen der Form und Farbe, Angaben zur Adult- und Geburtskörperlänge sowie zum Körpergewicht; 4. Identifikationskriterien im Lebensraum und 5. dessen Beschreibung; 6. Angaben zur Verbreitung und Wanderung der Art nebst einer Verbreitungskarte; 7. Nahrung und Nahrungsaufnahme; 8. Verhalten; 9. Fortpflanzung und Entwicklung sowie 10. Angaben zum Weltbestand und 11. zum Einfluß des Menschen auf die Art.

Alle, die sich für die faszinierenden Meeressäuger interessieren, können sich mit Hilfe des sehr preiswerten Buches sachlich korrekt und spannend informieren lassen. Dieses Buch ist nicht nur als Nachschlagewerk, sondern auch zum Schmökern sehr zu empfehlen. P. LANGER, Gießen

Subscription information for USA, Canada and Mexiko obtainable from Paul Parey Scientific Publishers, PO Box 1815, New York, NY 10156-0610, USA. Phone (212) 679–0782, Telefax (212) 213–3798.

Erscheinungsweise und Bezugspreis 1992: 6 Hefte bilden einen Band. Jahresabonnement Inland: 358,– DM zuzüglich 13,80 DM Versandkosten, Gesamtpreis 371,80 DM einschließlich 7 % Mehrwertsteuer. Jahresabonnement Ausland: 358,– DM zuzüglich 18,– DM Versandkosten. Das Abonnement wird zum Jahresanfang berechnet und zur Zahlung fällig. Es verlängert sich stillschweigend, wenn nicht spätestens am 15. November eine Abbestellung im Verlag vorliegt. Die Zeitschrift kann bei jeder Buchhandlung oder bei der Verlagsbuchhandlung Paul Parey, Spitalerstraße 12, W-2000 Hamburg 1, Bundesrepublik Deutschland, bestellt werden. Die Mitglieder der „Deutschen Gesellschaft für Säugetierkunde" erhalten die Zeitschrift unberechnet im Rahmen des Mitgliedsbeitrages.

Z. Säugetierkunde 57 (1992) 5, 257–320

Pareys Studientexte 66

Walter Pflumm

Biologie der Säugetiere

Von Prof. Dr. Walter Pflumm, Kaiserslautern. Pareys Studientexte, Bd. 66. 1989. 565 Seiten mit 413 Abbildungen und 4 Tabellen. Kartoniert DM 58,–.
ISBN 3-489-63534-5.

Im Zeitalter der Molekularbiologie und Biochemie hat die Säugetierkunde nicht an allen deutschsprachigen akademischen Ausbildungsstätten, aber auch in den Leistungskursen der reformierten Sekundarstufe den Stellenwert, der Ihr gerade in bezug auf das direkt auf den Menschen übertragbare Wissen, zukommt. Auch fehlte es bisher an einer geeigneten Darstellung des Stoffgebietes für die Lernenden. Diesem Defizit will das vorliegende Buch abhelfen. Mit subjektiver Stoffauswahl und guter didaktischer Darbietung ist es umfangreicher als die üblichen Hochschultexte und zugleich eines der am reichhaltigsten bebilderten Lehrbücher in der Biologie.

Das Buch behandelt ausführlich die Schlüsselmerkmale der Säugetiere, z. B. die Struktur und Funktion von Milchdrüsen und Haaren, und zwar von der zellulären Ebene bis zum Verhalten. Darüber hinaus werden Leistungen, die im übrigen Tierreich nur gelegentlich vorkommen, besonders gründlich dargestellt, so die Echo-Ortung und der Winterschlaf. Weitere Kapitel beschäftigen sich mit ontogenetischen Problemen. Auf biochemische und biophysikalische Sachverhalte wird dann eingegangen, wenn es sich um für Säugetiere spezifische Leistungen handelt. – Ein Verzeichnis mit Erklärungen der zoologischen Fachwörter, besonders wichtig für Leser ohne Latein- oder Griechischkenntnisse, sowie zwei Tiernamenverzeichnisse, ein Sachregister und ein Literaturverzeichnis machen das Buch von vielen Fragestellungen her zugänglich für einen großen Leserkreis. Dazu gehören Studierende der Biologie und Oberschüler der Sekundarstufe II ebenso wie Biologielehrer, Ausbilder von Tierpflegern und alle Natur- und Tierfreunde, die an einer umfassenden, in Wort und Bild leichtverständlichen Darstellung von Bau und Leben der Säugetiere interessiert sind.



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Die Zeitschrift für Säugetierkunde veröffentlicht Originalarbeiten und wissenschaftliche Kurzmitteilungen aus dem Gesamtgebiet der Säugetierkunde, Besprechungen der wichtigsten internationalen Literatur sowie die Bekanntmachungen der Deutschen Gesellschaft für Säugetierkunde. Verantwortlicher Schriftleiter im Sinne des Hamburgischen Pressegesetzes ist Prof. Dr. Dieter Kruska.

Zusätzlich erscheint einmal im Jahr ein Heft mit den Abstracts der Vorträge, die auf der jeweiligen Hauptversammlung der Deutschen Gesellschaft für Säugetierkunde gehalten werden. Sie werden als Supplement dem betreffenden Jahrgang der Zeitschrift zugeordnet. Verantwortlich für ihren Inhalt sind ausschließlich die Autoren der Abstracts.

Manuskripte: Manuskriptsendungen sind zu richten an die Schriftleitung, z. Hd. Prof. Dr. Dieter Kruska, Institut für Haustierkunde, Biologie-Zentrum, Neue Universität, Olshausenstr. 40–60, W-2300 Kiel, Bundesrepublik Deutschland. Für die Publikation vorgesehene Manuskripte sollen gemäß den „Redaktionellen Richtlinien" abgefaßt werden. In ihnen finden sich weitere Hinweise zur Annahme von Manuskripten, Bedingungen für die Veröffentlichung und die Drucklegung, ferner Richtlinien für die Abfassung eines Abstracts und eine Korrekturzeichentabelle. Die Richtlinien sind auf Anfrage bei der Schriftleitung und dem Verlag erhältlich.

Sonderdrucke: Anstelle einer Unkostenvergütung erhalten die Verfasser von Originalbeiträgen und Wissenschaftlichen Kurzmitteilungen 50 unberechnete Sonderdrucke. Mehrbedarf steht gegen Berechnung zur Verfügung, jedoch muß die Bestellung spätestens mit der Rücksendung der Korrekturfahnen erfolgen.

Fortsetzung 3. Umschlagseite

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On the hardness of pigmented and unpigmented enamel in teeth of shrews of the genera *Sorex* and *Crocidura* (Mammalia, Soricidae)

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The hardness of the enamel in the incisors of three species of shrew, *Sorex araneus, S. minutus* and *Crocidura russula,* was tested using a special ultra-low load indentation instrument. Two different measuring areas were selected; the first area was situated in the anterior part of the incisor (covered with pigmented enamel in the *Sorex* spp.), the second area was in the posterior unpigmented part of the same tooth. Large local variations in the mechanical properties occur, and possible reasons for these are discussed. The results do not clearly confirm any hypothesis concerning differences in hardness between the pigmented and unpigmented enamel, although there is some tendency showing the unpigmented enamel to be slightly harder than the pigmented.

Introduction

The teeth of most shrews in the subfamily Soricinae are partly covered with reddish tooth pigment. The reddish colouring is most prominent on the labial part of the teeth and on the occlusal part of the molars. This colouring is due to the presence of iron (DÖTSCH and VON KOENIGSWALD 1978). The iron is confined to the outermost zone of the enamel. Pigmented enamel is also known in rodents (MILES 1963) and also in this case iron is present (SELVIG and HALSE 1975). Tooth pigment was present already in some fossil shrews from the Miocene (CROCHET 1975), but in this case we deal with members of another subfamily (REUMER 1987). It has been postulated that the iron-containing enamel should be harder than the white enamel (SELVIG and HALSE 1975) and thus function as a protection against abrasion (VOGEL 1984; DANNELID 1989). However, DÖTSCH (1982, pers. comm.) suggests that the iron-containing enamel is weaker than the unpigmented parts. The pigmented enamel is also said to be more acid resistant than the white enamel (SELVIG and HALSE 1975). Acid resistance was, however, outside the scope of this paper.

To the present authors' knowledge no direct studies of the mechanical properties, such as hardness, have been performed. This is certainly due to the difficulties of making adequate measurements in small volumes of material. However, a new type of sub-micron indentation system has recently been developed (PETHICA et al. 1983), built on the principle of a continuous and very precise reading of load and displacement. This system is particularily well suited for investigations of small specimens, such as the enamel of shrew teeth. In this study we have measured the hardness of both types of enamel on shrew teeth to see whether any distinction in hardness is apparent.

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Material and methods

The hardness of the incisors of the lower left jaws of three different species of shrews, *Sorex araneus, S. minutus* and *Crocidura russula*, was measured. The two former species have the teeth partly covered with reddish enamel containing iron. *C. russula* has a very low content of iron in the enamel (Vogel, pers. comm.) and was chosen for comparison.

The jaws were from museum specimens and therefore needed a careful treatment. They were mounted on a specimen holder by water-soluble glue and then indented as-recieved, even though a conventional specimen preparation with embedding and polishing of a cross-section would have been preferred. Three different specimens of each species were tested. The measurements were performed at two different positions of each incisor (Fig. 1); on an anterior part of the incisor, in the iron-

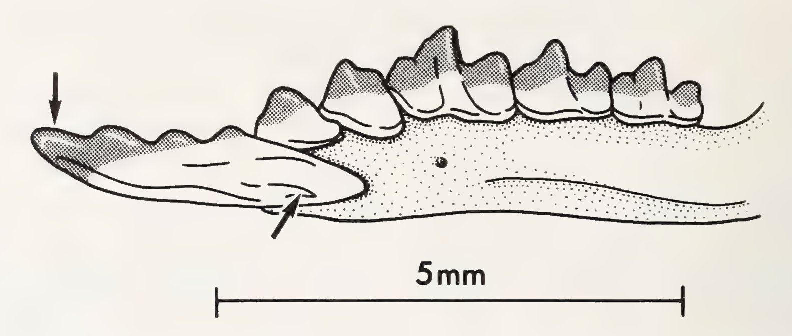


Fig. 1. Part of anterior left lower jaw of *S. araneus* with the measured areas indicated

containing area in the *Sorex* spp. or the corresponding area in *C. russula* (A), as well as in a more posterior position (B). At each position of the specimens several indentations were done, either in a line or in an ordered array.

The tests were performed with a special depth-sensitive indentation instrument (Nano indenter, Nano Systems Inc., TN, USA). The construction of the equipment and methods of analysis are described in detail elsewhere (Pethica et al. 1983; Doerner and Nix 1986). A schematic diagram of the indentation system is shown in Figure 2. The load is provided by a magnet and coil assembly and the corresponding displacement is continuously measured by the movement of the middle plate of a three-plate capacitance system. The depth-sensing mechanism makes optical imaging of the indentation unnecessary for the determination of the hardness, and in addition information from both the loading and the unloading sections of the experiment is recorded. The system is computer controlled and each indentation can be performed in an exact way by setting the approach rate, loading and unloading rate, time of hold and maximum load or displacement. The load and displacement resolutions are 0.3 μN and 0.2 nm, respectively.

In this study indentations were made with maximum displacements of 100 and 250 nm, i.e. the maximum depth of indentation is only a fraction of the expected thickness of the pigmented part of the enamel of 40–50 μm (Miles 1963; Vogel 1984). The loading and unloading rates were 10 nm/s. A 30 s hold segment (a segment during which the load is held constant for a certain period of time) was applied at maximum load and at 90 % of unloading to check the thermal drift. The result from a single indentation experiment is typically presented as a load-displacement curve (Fig. 3). The hardness is calculated as the maximum load divided by the area of the indentation after subtraction of elastic contributions.

The microstructure was studied and a qualitative elemental analysis of the enamel was done using a scanning electron microscope (SEM – JSM-840, JEOL Ltd, Tokyo, Japan) equipped with an energy dispersive spectrometer (EDS – LINK AN 10 000, Link Analytical Systems Ltd, High Wycombe, UK).

Results

The nanoindentation system is very sensitive to differences in height across the specimen, as well as to unevennesses in the specimen surface. Nevertheless, the method of specimen mounting worked satisfactorily as long as the indentations were placed on nearly horizontal areas close to the highest point of the samples. The surfaces of the teeth at the microlevel

Fig. 2. Schematic diagram of the indentation system (from SÖDERLUND and MACMILLAN 1991)

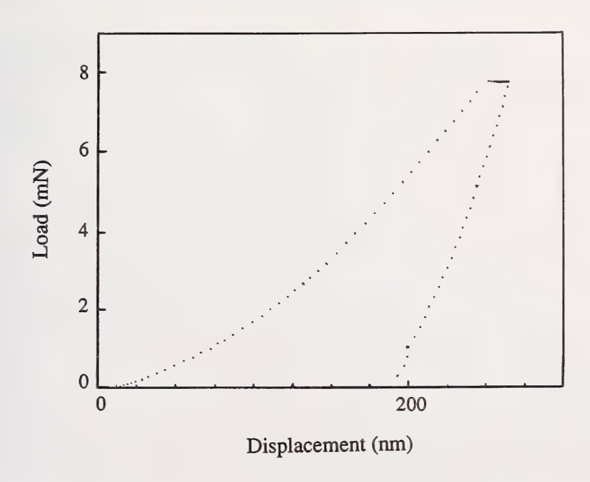


Fig. 3. Typical load-displacement curve obtained from a 250 nm indentation in the unpigmented enamel of a *S. araneus* specimen

are very rough (Fig. 4), but the load-displacement curves reveal any tendency of sliding of the indenter or other abnormality and such indentations were then disregarded. The thermal drift in the system was measured and was typically less than 0.05 nm/s.

Most of the hardness data lay in the regime 6–9 GPa (hereafter called the high regime) and in some cases around 0.1–0.4 GPa (henceforth named the low regime) for a 100 nm deep impression. Values obtained from 250 nm deep indentations were of the order 4–7 GPa or lay in the same low regime of 0.1–0.4 GPa. The hardness data obtained from one of the *S. minutus* specimens lay only in the low regime. The data points in Figure 5 are the

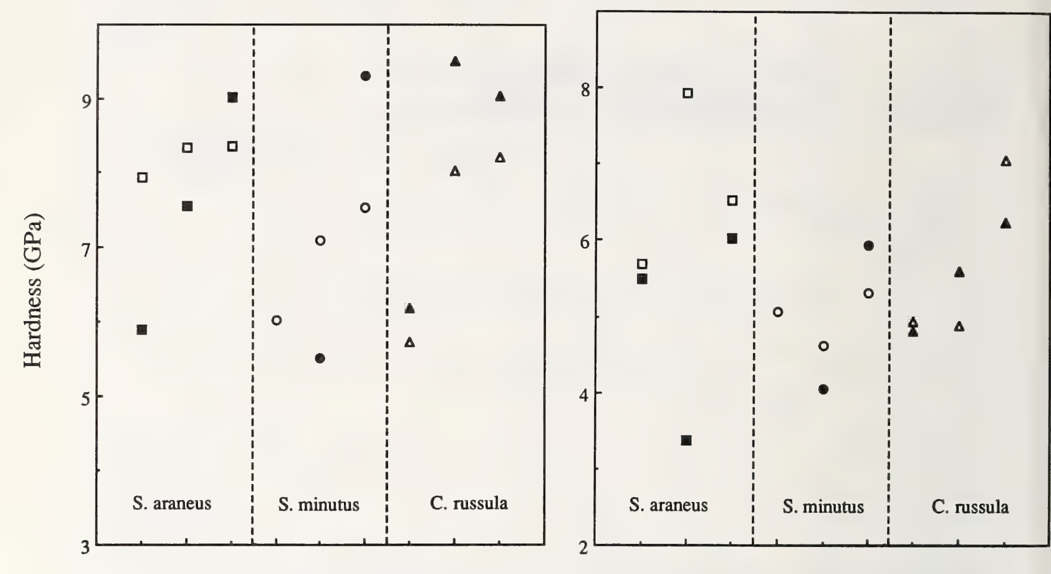
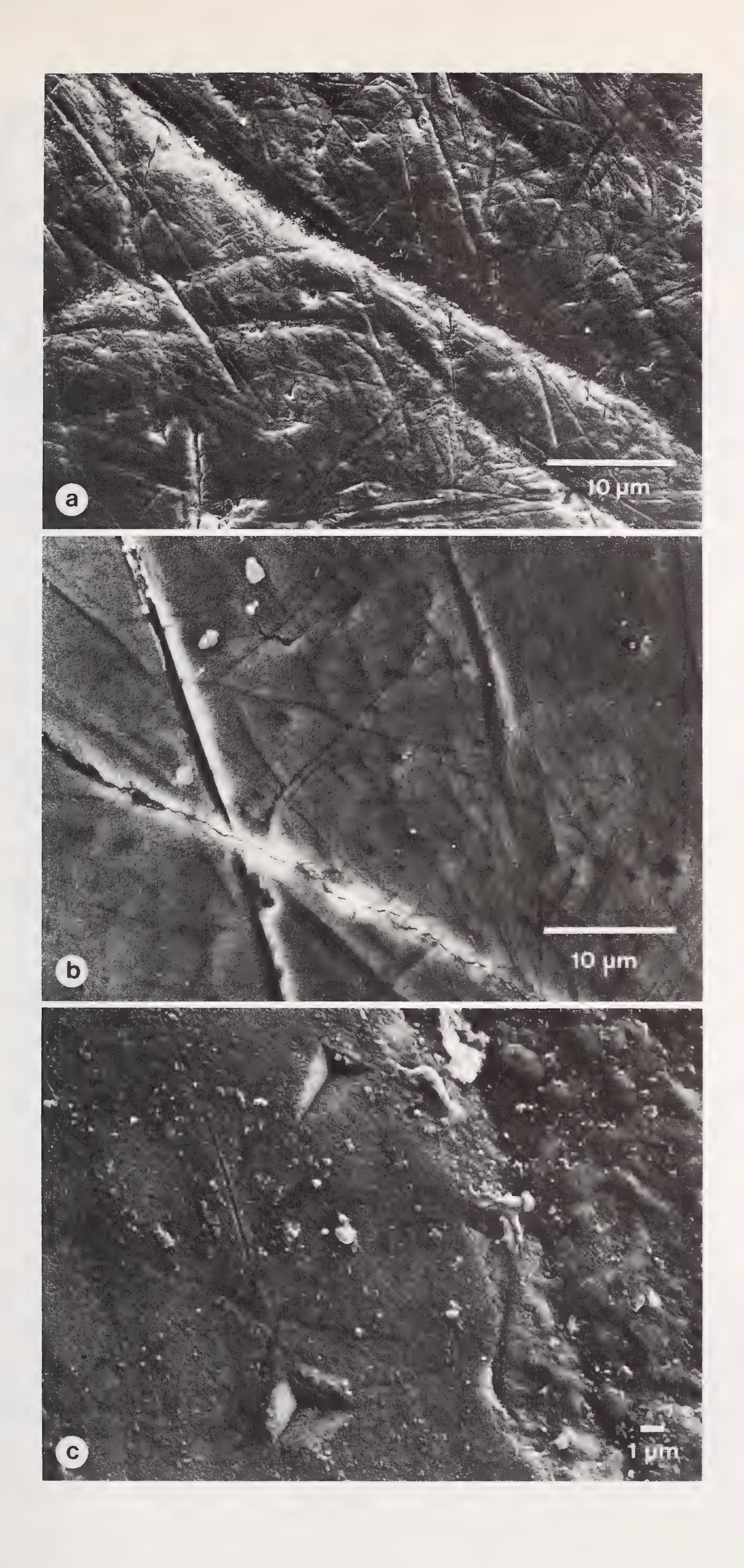


Fig. 5. The average hardness (high regime) obtained from area A of each specimen (filled symbols) and from area B (unfilled symbols) for the two indentation depths 100 nm (a) and 250 nm (b)

averages of the high regime values obtained at each position of each specimen. The Table presents the mean high regime values together with one standard deviation and the number of valid indentations. The percentage of the total number of indentations that lay in the low hardness regime for each region is seen in the Table. The values in the low regime could not be used for comparative purposes for several reasons, which are discussed in the next section.

The SEM study revealed that the surface of the enamel was rough (Fig. 4). Commonly, the enamel was very scratched and cracks could be seen. Occasionally the enamel had fractured and pieces of the enamel were missing. The *S. minutus* specimen with hardness values only in the low regime, seemed to be covered with a thin film. However, no difference in composition could be detected by EDS, between areas of enamel with or without the film. By the EDS analysis it was confined that the pigmented areas were rich in iron. In areas where the iron content was higher than the surroundings, the concentration of calcium was correspondingly lower. The oxygen concentration was enhanced in the same areas as the iron.

Fig. 4. SEM micrographs of a *S. araneus* specimen showing (a) the microstructure of the pigmented enamel (position A), (b) the microstructure of the unpigmented enamel (position B), and (c) two of the indentations made in position A


10 µm
a
10 µm
b
1 µm
c

Average of hardness (high regime), standard deviation and number of indentations for the two regions tested at each specimen

Specimen and species	Measured area on tooth	Hardness (in GPa)	Standard deviation (in GPa)	Number of indentations	Indentations in the low regime (% of total number)
		Indentation depth = 100 nm			
S. araneus 1	A	5.88	1.27	10	31.3
S. araneus 1	B	7.93	1.45	8	20.0
S. araneus 2	A	7.55	2.31	5	0.0
S. araneus 2	B	8.34	0.99	5	0.0
S. araneus 3	A	9.01	2.49	19	56.4
S. araneus 3	B	8.36	2.85	18	5.0
S. minutus 1	A	–	–	8	97.4
S. minutus 1	B	6.01	1.70	5	61.5
S. minutus 2	A	5.51	1.45	8	20.0
S. minutus 2	B	7.09	1.72	8	65.0
S. minutus 3	A	9.30	2.72	13	28.6
S. minutus 3	B	7.54	0.59	7	10.0
C. russula 1	A	6.18	1.89	9	55.0
C. russula 1	B	5.72	0.93	11	20.0
C. russula 2	A	9.51	3.56	10	0.0
C. russula 2	B	8.03	1.03	7	10.0
C. russula 3	A	9.04	3.65	8	30.0
C. russula 3	B	8.21	1.34	7	0.0
		Indentation depth = 250 nm			
S. araneus 1	A	5.50	1.54	7	0.0
S. araneus 1	B	5.69	0.82	9	0.0
S. araneus 2	A	3.38	0.74	5	0.0
S. araneus 2	B	7.93	1.62	4	0.0
S. araneus 3	A	6.03	1.35	14	34.6
S. araneus 3	B	6.52	0.88	16	0.0
S. minutus 1	A	–	–	8	94.9
S. minutus 1	B	5.06	1.71	8	0.0
S. minutus 2	A	4.04	1.10	9	10.0
S. minutus 2	B	4.62	0.78	12	40.0
S. minutus 3	A	5.93	0.77	4	20.0
S. minutus 3	B	5.32	0.52	9	10.0
C. russula 1	A	4.82	0.93	13	35.0
C. russula 1	B	4.94	1.09	15	0.0
C. russula 2	A	5.59	2.11	10	0.0
C. russula 2	B	4.89	1.04	9	10.0
C. russula 3	A	6.24	1.18	10	0.0
C. russula 3	B	7.06	1.29	10	0.0

Discussion

The large scatter in the hardness data indicates a substantial inhomogeneity in the surface properties. In particular the occurrence of the low and high hardness regimes can only be interpreted as arising from different materials. We suggest that the high hardness regime reflects the hardness of more or less undamaged enamel, whereas the low hardness sites would occur if the enamel was covered with a thin, soft film or locally absent and the impressions were then being made in the underlying softer structure. For this reason the low regime values are not considered further in this study.

The different mean levels of the high regime hardness values corresponding to the two

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indentation depths, 100 nm and 250 nm, stem from the fact that hardness determined by an indentation method shows a strong increase with decreasing indentation depth (see for example, BULL et al. 1989). Therefore, the 100 nm values are larger than the 250 nm values and neither of the data sets can be directly compared with micro- or macro-hardness (bulk) values. Due to the indentation size effect only values obtained from indentations with the same maximum indentation depth should be compared in detail.

In *C. russula,* which has unpigmented teeth, only in one test out of six was there any significant difference in hardness between the two areas investigated. This uniformity is as expected. In the *Sorex* spp., however, clear differences occasionally occur. With an indentation depth of 100 nm, one specimen of *Sorex araneus* showed a distinctly harder white enamel. In *Sorex minutus* there was one specimen with harder unpigmented enamel and one specimen with harder pigmented enamel.

The third specimen of *S. minutus* showed a hardness of the pigmented area which was almost exclusively situated in the low regime (four different positions were investigated with 39 indents and only 1 showed high regime hardness). When the indentation depth increased to 250 nm, most *Sorex* specimens showed a harder white enamel. In all cases except two, when going from 100 nm deep to 250 nm deep indentations, the region A showed a relative decrease in hardness as compared to region B. This might be due to an increased influence from the softer underlying substrate, or a decreased influence from a soft film. No obvious difference in hardness between the red enamel of *S. araneus* and *S. minutus* could be seen from out tests though *S. araneus* has a clearly darker pigment than *S. minutus*.

The large variations in hardness, both within a single specimen (reflected as a substantial standard deviation) as well as between specimens of the same species, may have several possible reasons. One is of course that the teeth may be considerably worn at one or more of the measuring areas. However, all the specimens were first year animals without apparent tooth wear (all specimens were checked in a dissecting microscope before fixation, to avoid severely worn teeth). KOZAWA et al. (1988) have proposed that the iron may exist in three different forms in the pigmented enamel; firstly, as an amorphous ferric oxide around the hydroxyapatite crystallites, secondly as iron atoms in the hydroxyapatite lattice, and thirdly as crystalline iron oxide on the crystal surface. In the first of these, the pigmented enamel may well be weaker than the unpigmented; in the second case probably harder, since the iron ions are smaller than the calcium ions, which (with constant charge) means denser packing and shorter bond lengths (VINCENT 1990). The EDS analysis performed by us indicates that some iron probably substitutes for calcium in the apatite structure. The observed higher level of oxygen could indicate that some iron is also present in the form of iron oxide. KOZAWA et al. (1988) also found a variable Ca/P ratio in the enamel of the *Sorex* specimens (compared to human enamel and F-apatite) which suggests a non-uniform composition of the enamel crystallites. Furthermore, they observed the existence of carbonate in the unpigmented enamel and in microareas of the pigmented enamel, which may indicate a low degree of crystallinity in the enamel. This would possibly affect the hardness and give rise to local variations.

Thus the results do not confirm the hypothesis that iron-containing pigmented enamel should be harder than unpigmented. The local variations in enamel hardness within a specimen as well as the variations between specimens are larger than any clear differentiation in hardness due to presence of iron in the enamel.

Finally, a harder material is usually more resistant to abrasion, but for ceramic materials this is not always true. An increased hardness might lower the threshold load above which cracking (median and lateral) and chipping, and a corresponding severe wear, occur (EVANS and MARSHALL 1980). For loads below the fracture threshold, no cracking occurs and the ceramic is worn by a plastic cutting mechanism, the volume removal rate of which is about one order of magnitude lower than that associated with the lateral fracture mechanism.

Accordingly, a lowered hardness might cause a transformation from a severe wear mechanism, to a milder wearing. Another important parameter, that will also strongly affect the threshold load and determine the wear rate, is the fracture toughness (a measure of the resistance to cracking). We have not taken the fracture toughness into consideration in this investigation, however, there might be possible toughening effects due to the three postulated different occurrences of iron in the pigmented enamel.

Both the pigmented and the unpigmented enamel of all specimens show large local variations in hardness. The nanoindentation hardness for a 100 nm deep indent usually is 6–9 GPa or 0.1–0.4 GPa depending on which region measured. The variation in the results may be explained by different forms of iron in the pigmented enamel, by varying composition of the apatite crystallites, by a varying degree of crystallinity in the enamel as well as by the local wear status. However, there is no clear difference in hardness between the pigmented and the unpigmented enamel, even though there is some tendency showing that the unpigmented enamel is slightly harder than the pigmented.

The nanoindenter system is well suited for this type of investigation since it can obtain information from near surface regions of the order of 1 µm. This particular material shows variations in the local properties larger than in synthetic hydroxyapatite, and uniformly polished surfaces and cross-sections would therefore be needed for a more thorough investigation.

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Zusammenfassung

Über die Härte von pigmentiertem und unpigmentiertem Zahnschmelz bei Spitzmäusen der Gattungen Sorex und Crocidura (Mammalia, Soricidae)

Die Härte des Zahnschmelzes in den Schneidezähnen von drei Spitzmausarten, *Sorex araneus, S. minutus* und *Crocidura russula,* wurde mit einem speziellen Gerät getestet, welches den Zahn einer äußerst geringen Belastung aussetzt. Zwei verschiedene Regionen wurden vermessen, die erst in dem vorderen Teil der Schneidezahnes (bei den *Sorex*-Arten mit pigmentiertem Zahnschmelz überzogen), die zweite in der hinteren, unpigmentierten Region desselben Zahnes. Es bestehen große lokale Unterschiede in den mechanischen Eigenschaften und mögliche Ursachen dafür werden diskutiert. Die Resultate bekräftigen keine Hypothese über Unterschiede in der Härte des pigmentierten gegenüber dem unpigmentierten Zahnschmelz. Es gibt jedoch eine Tendenz dahin, daß der unpigmentierte Zahnschmelz etwas härter ist als der pigmentierte.

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G-, C-bands and NOR studies in two species of bats from Southern Brazil (Chiroptera: Vespertilionidae, Molossidae)

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Abstract

Described the karyotypes of two species of bats from Southern Brazil, *Eptesicus brasiliensis* (2n = 50; AN = 48) and *Molossus molossus* (2n = 48; AN = 54). The study of *E. brasiliensis* was based in seven males and seven females, while that of *M. molossus* included three males and 13 females. All autosomal chromosomes of *E. brasiliensis* are acrocentric, while *M. molossus* presents four pairs of submetacentric and 19 pairs of acrocentric chromosomes. Both species present an acrocentric Y chromosome; the X is submetacentric in *E. brasiliensis* and metacentric in *M. molossus*. The G-bands of *E. brasiliensis* do not differ markedly from those reported for other species of *Eptesicus*. *M. molossus*, however, presents a rather different G-pattern from those of other species of the same family. As for the C-bands, the results for both species are not remarkably different from those of other species of the same families. *E. brasiliensis* and *M. molossus* show a nucleolus organizing region (NOR) in only one pair, the one that presents a secondary constriction near the centromere.

Introduction

The bats present in the Southern Brazilian state of Rio Grande do Sul inhabit an area between two subregions of the Neotropical region, the Brazilian Highlands and Coast, and Patagonia. Eleven species of the family Vespertilionidae and eight of the Molossidae have been reported to live in the state (Silva 1985). This work deals with *Eptesicus brasiliensis* (Vespertilionidae) and *Molossus molossus* (Molossidae), bats which are distributed over all South America (Koopman 1982). Previous studies on these species report a diploid number (2n) equal to 50 for *E. brasiliensis* (Ando et al. 1977; Williams 1978; Bickham 1979; Volleth 1987), and 2n = 48 for *M. molossus* (Baker and Lopez 1970; Warner et al. 1974), but no chromosome bands or NOR observations were made on them. The objective of this study was to fill this gap in our knowledge.

Material and methods

Fourteen specimens of *Eptesicus brasiliensis* (Desmarest, 1819) were studied, seven males and seven females from Fazenda Caçapava, in Taim's Ecological Station (32° 32′S; 52° 32′W). The sample of *M. molossus* (Pallas, 1766) is constituted by 16 specimens, two males and 10 females from this same place, one male from Porto Alegre (30° 10′S; 51° 15′W), and three females from Torres (29° 21′S; 49° 46′W), all localities in the Brazilian state of Rio Grande do Sul.

Lee and Elder's (1980) technique was employed in the bone marrow chromosome preparations. The G-bands were induced following Seabright's (1971) method with the modifications proposed by Patton and Baker (1978), while the C-band patterns were obtained with Sumner's (1972) technique. The NOR observations were made using Howell and Black's (1980) method.

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Results

Eptesicus brasiliensis presented 2n = 50 with an autosomal arm number (AN) equal to 48. Figure 1a shows the standard karyotype of this species. All the autosomes are acrocentric, roughly classifiable in large (pairs 1 to 15), median (pairs 16 to 21), and small (pairs 22 to 24) chromosomes. The X is a median submetacentric and the Y is a small acrocentric. Figure 1b presents the patterns of constitutive heterochromatin for this species. There are well defined, small C-bands in pairs 3 to 8, 10 to 13, 16, 18, 20 and 21, representing 58 % of the autosomes with marked centromeres. The X chromosome also has a C-band, while the Y is totally heterochromatic. G-bands are shown in Figure 1c, while Figure 1d presents the nucleolar organizer region in pair 14, which has a secondary constriction near the centromere (Fig. 1a).

M. molossus has 2n = 48 and AN = 54. Conventional staining (Fig. 1e) shows four pairs of submetacentric chromosomes, pair 1 being the larger; the other three are median submetacentrics, while the remaining autosomes are all acrocentric. Pairs 22 and 23 are very small compared to the rest of the karyotype. The X chromosome is a median metacentric, a little larger than pairs 2–4, while the Y is a small acrocentric. C- and G-band patterns are shown in Figures 1f and 1g, respectively. C-bands occur in almost all autosome pairs, the exception being pair 7, and in the X. The nucleolar organizer region (Fig. 1h) occurs in pair 8 at the secondary constriction near the centromere.

Discussion

Eptesicus brasiliensis

The genus *Eptesicus* comprises about 30 species worldwide (Emmons 1990). Approximately 50 % of them present 2n = 50 and AN = 48 (Ando et al. 1977; Williams 1978; Zima 1982; Volleth 1987; Varella-Garcia et al. 1989), but others show reduced chromosome numbers (for instance, *E. capensis* with 2n = 32, AN = 50; *E. zulensis* with 2n = 28, AN = 48). Species with different chromosome numbers, however, are morphologically similar (McBee et al. 1986; McBee et al. 1987; Morales et al. 1991). We found 2n = 50 and AN = 48 for *E. brasiliensis* from Rio Grande do Sul, thus agreeing with Bickham (1979) who found the same numbers studying specimens from the Nearctic region.

No remarkable differences were found between the G-bands presented here and those found by Zima (1982) in *E. nilssoni*. This fact, and the relative constancy in chromosome numbers, demonstrates that this genus is chromosomically conservative. In relation to the C-bands, we found only 58 % of autosome pairs marked, while Ando et al. (1980) determined low quantities of constitutive heterochromatin for other species of Vespertilionidae. Only pair 12 of *E. brasiliensis* showed a nucleolar organizer region, in accordance with the findings in *E. serotinis* (Volleth 1987).

Molossus molossus

Five diploid numbers were reported within the family Molossidae: 2n = 34, 38, 40, 42, and 48 (Baker et al. 1982; Varella-Garcia et al. 1989). The 2n = 48 karyotype is the most frequently found. Warner et al. (1974) found 2n = 48 and AN = 58, while Baker and Lopez (1970) reported 2n = 48 and AN = 56 for *M. molossus* of North and Central America, respectively. We observed 2n = 48, AN = 54. This suggests variation due to pericentric inversions, but since no banding was performed in these earlier studies, we cannot be sure about that.

For the C-bands, our results are not too different from those reported by Morielle-Versute et al. (1991). These authors studied two species of the genus *Molossops: M.*

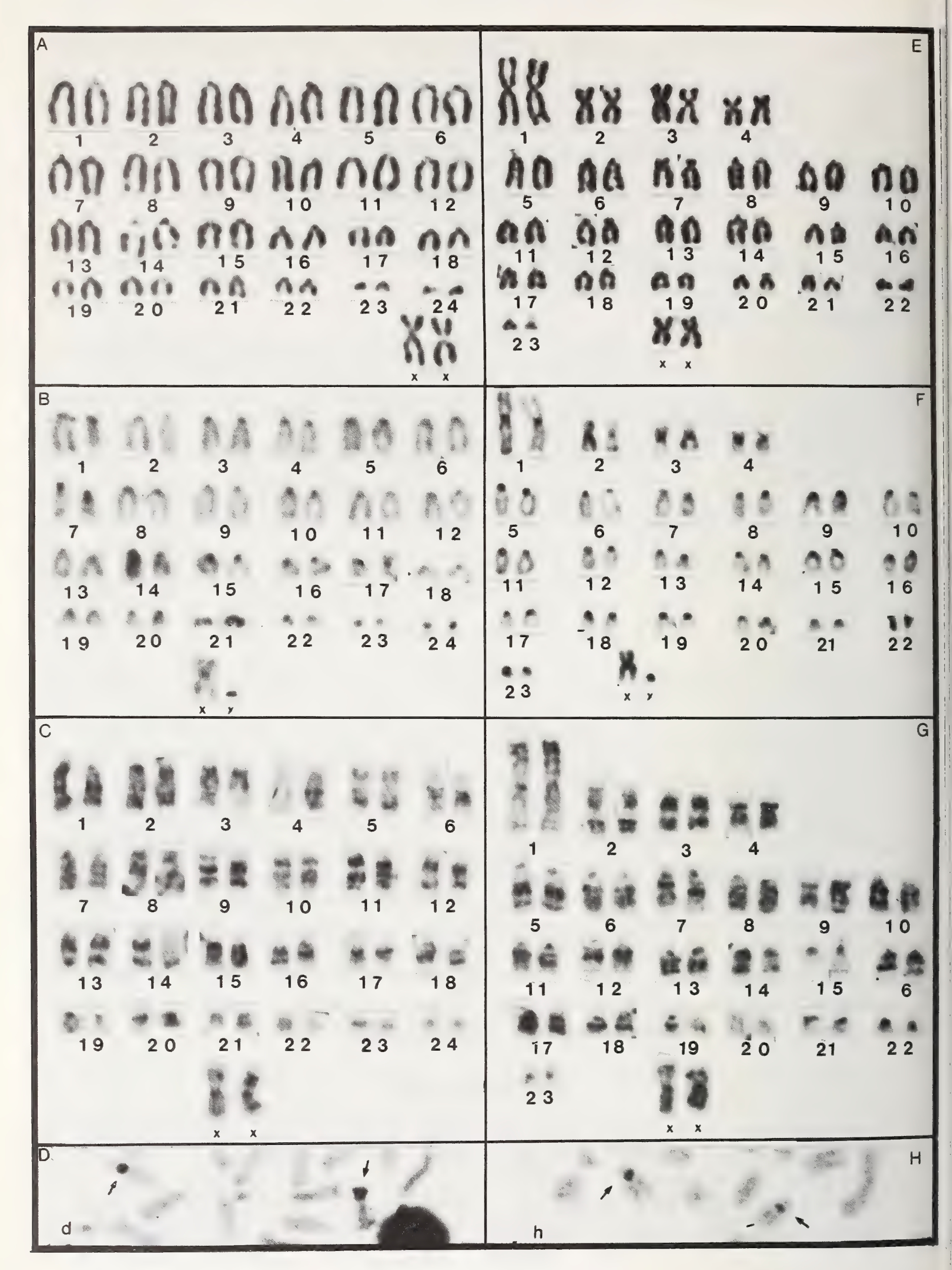


Fig. 1. Chromosomes of *E. brasiliensis.* A: Standard bone marrow Giemsa stained karyotype; B: C-bands; C: G-bands; D: NOR identification. E–H: Chromosomes of *M. molossus.* E: Giemsa stained karyotype; F: C-bands; G: G-bands; H: NOR identification

abrasus and *M. temminckii*. Both showed C-bands in all centromeres. Additionaly *M. abrasus* presented a C-band in the telomeric region of the short arms of the largest acrocentric pair, and *M. temminckii* a C-band in the satellite region of the short arm of a large acrocentric pair. We found in *Molossus molossus* blocks of pericentromeric constitutive heterochromatin in 22 of the 23 autosome pairs and in the X. However, this species presents rather different G-bands from those reported for *M. abrasus* and *M. temminckii*. In addition, nucleolar organizing regions were found in one pair in *M. molossus* while *M. abrasus* presented such regions in five small chromosomes, and *M. temminckii* in three pairs.

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Zusammenfassung

G-, C- und NOR-angefärbte Karyotypen von zwei Fledermausarten aus Südbrasilien (Chiroptera: Vespertilionidae, Molossidae)

Es werden Standardkaryogramme sowie G-, C- und NOR-gefärbte Metaphasen von zwei Fledermausarten aus Südbrasilien beschrieben. Je 7 Männchen und Weibchen von *Eptesicus brasiliensis* (Vespertilionidae) und 3 Männchen und 13 Weibchen von *Molossus molossus* (Molossidae) wurden untersucht. Die cytogenetische Analyse ergab 2n = 50 and AN = 48 für *E. brasiliensis* and 2n = 48 and AN = 54 für *M. molossus*. Bei *E. brasiliensis* sind alle Autosomen akrozentrisch; *M. molossus* weist 4 Paare submetazentrischer und 19 Paare akrozentrischer Chromosomen auf. Beide Arten haben ein akrozentrisches Y-Chromosom, das X-Chromosom ist submetazentrisch bei *E. brasiliensis* and metazentrisch bei *M. molossus*. Die Muster der G-Bänder bei *E. brasiliensis* unterscheiden sich nicht von denen anderer *Eptesicus*-Arten. Dagegen unterscheidet sich *M. molossus* deutlich von anderen Arten der Familie. Bei den C-Bändern ergaben sich keine wesentlichen Unterschiede. Bei beiden Arten ließen sich NORs nur in einem Chromosom anfärben, welches eine sekundäre Einschnürung in der Nähe des Centromers aufweist.

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Observations on the postnatal behavioural development in the Marsh mongoose (*Atilax paludinosus*)

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Abstract

Marsh mongooses (*Atilax paludinosus*) are solitary, nocturnal herpestines. This study describes postnatal behaviour patterns in naturally reared and hand-raised animals. First appearance of nine different categories was recorded. Comparisons were made with postnatal behavioural development in other herpestines, in order to assess to what extent it reflects the phylogeny of the subfamily.

Introduction

Postnatal physical development in marsh mongooses is documented (Frese 1980; Baker and Meester 1986), but there is no literature on postnatal behavioural development. Unlike the more sociable Herpestinae, *Atilax* is solitary and shows no co-operative behaviour in raising young. Differences in the development of postnatal behaviour patterns amongst herpestines may be attributed to their divergent rearing systems. In order to investigate this suggestion, this study describes postnatal behaviour patterns of both naturally reared and hand-raised *Atilax*, and compares it with the rate and pattern of development in other herpestines.

Material and methods

The thirteen animals here reported on originated from five captive matings and two wild matings. Naturally reared mongooses were maintained in outdoor enclosures measuring 1.5 × 3 × 1.2 m, while hand-raised animals were reared indoors in a room measuring 2 × 3 m. The milk formula fed to hand-reared animals consisted of one part tinned, evaporated, unsweetened milk (brand name Carnation) to two parts of water. To each 500 mls of constituted milk compound, 5 mls of glucose and 2 mls of multivitamin syrup (brand name Vi-daylin) were added. Mongooses were bottle-fed, using miniature (30 ml capacity) glass bottles with rubber teats, at three- or four-hourly intervals for the first 14 days, and thereafter at four-hourly intervals during daylight hours only, until weaning commenced. During weaning feeds were spaced at five-hourly intervals. First solids offered to the mongooses were finely chopped oxheart and chicken. Naturally reared animals were undisturbed and entirely raised by their mother.

First appearance of behaviour patterns were recorded and descriptions of the patterns were made.

Results

Table 1 provides details of the mongooses described in this study. Concern over the survival of the young in the presence of the father prompted removal of two of the four male mongooses from the females as soon as pregnancy was established (Baker and Meester 1986). As a result these litters (A1 and E2) were exclusively reared by the mother. On three other occasions the males had access to the females during parturition. Firstly

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(litter B1), the male remained in the enclosure for three days after parturition but was excluded from the "nursery nestbox" by the female and played no role in rearing the offspring. Secondly (litter E1), three young were born, one of which was killed and eaten by the mother who was agitated by the presence of a male and female. The remaining two offspring survived as a result of hand-rearing. On the third occasion (litter G1) two young were removed for hand-raising when their littermate was found dead.

Table 1. **Details of the animals from which data were gathered**

Litters	Mating	Offspring ♂♂	Offspring ♀♀	Natural (N)/ Hand-reared (H)
A1	Captive	AA; AB	AC	N
B1	Captive		BA; BB	N
E1	Captive	EB	EA	H
E2	Captive	EC; ED		N
G1	Captive	F	D	H
–	Wild		E	H
–	Wild		K	H

Parturition occurred at night (between 18.30 h and 03.00 h), and in one instance (litter E1) it lasted 4.5 hours. The mother ate little or nothing of the normal food provided on the night of parturition. While activity patterns were normal until the evening of parturition, the female remained comparatively inactive during the birth, and remained within the nestbox. Nesting material was not used and on the completion of the birth the female remained with the young.

Maternal care involved suckling, stimulating excretion, protection and transmitting skills to the young. In the first few weeks the mother prompted elimination by licking the ano-genital region of her young, and then consumed the products. If the mother became agitated or was disturbed when she had a very young litter, she usually picked up a single youngster in a neck-grip or scruff-hold, and ran about the cage as if attempting to escape from the source of 'danger'.

In naturally reared litters, young became mobile outside the nestbox on day 23 at the earliest, but more commonly this happened only by day 28. As soon as exploration began, the mother kept a close watch over the young and, in the event of 'danger', she retrieved them by means of a scruff-hold, transporting them to the safety of the nestbox. As the young matured they became less docile and attempted to re-emerge as soon as the mother had retrieved them. On these occasions she simply blocked the nestbox entrance or held the young by the scruff until the 'danger' had passed. By day 61 the young avoided retrieval by the scruff-hold, and the mother attempted to 'herd' them back to safety. When 'herding' the mother directed the young by moving quickly beside them and nudging them forwards.

Table 2 provides details of the onset of behaviour patterns exhibited by both naturally reared and hand-reared mongooses. Apart from sucking and attention vocalizations (the attention call and grizzling), crawling and inefficient scratching, the alarm response was the earliest behaviour pattern to emerge. The feeding growl coincided with the development of weaning. Play became apparent as locomotory capacities improved, while the development of scent-marking was closely followed by the onset of cackle vocalizations. Sibling fighting and copulatory behaviour were the last behaviour patterns to develop.

While crawling was the first locomotory activity recorded, it was inefficient for the first few days. Young mongooses were scarcely able to lift the belly off the ground, and movement was shaky. Direction was random and only short distances were traversed. The grizzle vocalization accompanied all early forms of locomotion.

Table 2. **Average age (in days) of first appearance of postnatal behaviour patterns in *Atilax paludinosus***

Behaviour	Naturally-reared Mean age (days)		Hand-reared Mean age (days)		Significance (p = 0.05)	
Vocalizations						
Attention	–		0–38	n=2		
Grizzle	0	n=7	0	n=6		
Food	34.4	n=7	33.3	n=3	t=0.35	NS
Cackle	–		59	n=3		
Humph	88	n=2	–			
Bray	–		106	n=2		
Locomotion						
Crawl	0	n=7	0	n=6		
Run	31.1	n=7	27.3	n=3	t=1.59	NS
High-sit	53	n=6	43.3	n=3	t=5.08	S
Grooming						
Scratch	–		15.5	n=2		
Fleaing	–		23.5	n=2		
Lick	–		36	n=1		
Alarm	18	n=2	27	n=3	t=−0.77	NS
Feeding						
Wean	32.4	n=7	30.6	n=3	t=0.56	NS
Throw	62.5	n=6	98	n=4	t=−3.2	S
Prey kill (rodent)	121.8	n=5	140	n=2	t=−1.3	NS
(crab)			129	n=1		
Marking						
Urination	–		27.5	n=2	SD=0;	no t-test
Defaecation	31.8	n=7	35	n=2		
Anal marking	46.5	n=7	–			
Cheek marking	60	n=1	–			
Play						
Biting	29	n=5	29	n=3	t=0	NS
Dyadic	32.4	n=5	33.5	n=2	t=−0.29	NS
Object	26	n=2	38	n=1		
Mounting	–		202.5	n=2		
Copulation	295	n=5	256	n=1		
Sibling fighting	256	n=2	301	n=3	SD=0;	no t-test

In hand-raised mongooses grooming developed early, but scratching was inefficient during the first few days. By day 29 scratching was well co-ordinated. The fleaing response (Ewer 1963) resulted from rubbing the mongooses on either the tail base or the shoulder/neck area. Grooming was deemed effective from day 36 when the mongooses began tending to their pelage more carefully. Data regarding the development of grooming in naturally reared animals are lacking due to their confinement in the nestbox during the first few weeks.

The fear response involved several behavioural components, including mouth opening, a harsh abrupt expiration, and freezing (tonic immobility). One or more of these patterns occurred when the young were suddenly disturbed. The onset of the alarm response coincident with eye opening indicated that the stimulus was visual.

The beginning of weaning varied from day 29 to day 40 in naturally raised mongooses, and was not significantly different from the onset in hand-raised animals (Tab. 2). It was followed by a rapid increase in solid food intake. Suckling did not stop at the commencement of weaning, but was phased out over a long period, with some young still sucking the

mother's teats until day 108. The sucking response was particularly well-developed, as shown by a pair of hand-raised mongooses (EA and EB) that sucked on each other's genitalia in the absence of the mother's teats. This continued well beyound weaning, and was still observed when the pair (a male and a female) were ten months old.

When presented with live small mammal prey at 67 days of age (white mice) naturally raised young (AA, AB, AC) seemed unaware of the method of prey capture. The mother initially caught and killed the prey within view of her offspring, and then encouraged them to take it from her by shaking her head and drawing attention to the food. She relinquished the prey as soon as the young showed interest, and even appeared to encourage food envy by pulling away if interest in it waned. When live prey were introduced 30 days later, the mother held back and allowed the young to investigate it, and also attempt killing. Killing was not immediately achieved, and the young were more interested in playing with the injured animal. After approximately 20 min the mother dispatched the prey, and by virtue of her interference promoted food envy and consumption. Prey capture and killing was only achieved on day 135 in these mongooses. While naturally raised EC and ED captured their first prey at 102 days, killing was achieved incidentally over a long time by shaking and injuring the mice. Hand-raised mongooses (EA and EB) were given live prey at 140 days. The mice were bitten in the head region and killed in approximately 30 seconds, and then played with prior to consumption. Both hand-raised and naturally reared young began to eat from the anterior end. First encounters with *Xenopus* were different in that both naturally reared and hand-raised young encountered frogs in the ponds between 80 and 89 days, and immediately began to search for them by feeling over the pond substrate. When the frog was captured, possession was maintained by 'hip-slamming' and growling. Although a killing bite was not administered, the young dealt with the prey in adult fashion (Baker 1989).

The throwing response relates to the method used by some mongooses in immobilising crabs, as well as in egg-breaking. Throwing matured over approximately one month. It began with holding and fiddling with an object between the forefeet, with the mongoose lying either on its side or on its ventral surface; it progressed to lifting the object in the bipedal stance; then to dropping it often accidentally; and finally the intention of downward throwing developed. The discovery of the food content of the eggs was revealed by accidental egg-breaking in hand-raised mongooses, and by the mother breaking them open for her young in natural circumstances.

Discussion

Mortality in marsh mongoose litters has been recorded at Berlin Zoo by Frese (1980). Factors contributing to the deaths were suggested to be the presence of a conspecific of the same sex or lack of experience of the mother. While the effect of the presence of a male during parturition and the subsequent early development of the young was a cause for concern, it appeared that from eight weeks onwards the young and their mother suffered no ill-effects from the re-introduction of the male. The present study confirmed the adverse effects of the presence of more than one conspecific other than the mother (i.e. a male and a female) on the survival of a litter during parturition. On the other hand the presence of a single male during parturition and the following few days appeared to have no ill-effects. The male clearly did not participate in rearing the young, however, and it is unlikely that a male marsh mongoose which was actively avoided in the natural environment would remain in the vicinity of a mate with young. Exclusively maternal care seems more likely. The solitary nature of marsh mongooses, and the general lack of co-operative behaviour patterns, suggest that females habitually rear young in the absence of a partner. This contrasts strongly with the "helper" system which predomination in the more social

mongooses (dwarf mongooses – Rasa 1989; suricates – Ewer 1963; banded mongooses – Rood 1974).

In the nocturnal marsh mongoose the adaptiveness of parturition at night is clear, in that it would allow the mother to remain with her young for the daylight period following birth and perhaps longer, as the nourishment provided by the placental material is adequate to her needs for the first day. Further, the presence of the mother provides both security and nourishment for the young, so that when she does leave to forage the following evening the young are nutritionally satisfied and quiet. Hand-raised young which are not hungry remained asleep and quiet when new-born. When hungry, however, they vocalised loudly which would indicate their presence and attract would-be predators in the natural environment. Even in captivity the mother never abandoned her young for long periods during the first few weeks, and if she was away from the nestbox and heard the young vocalising she returned immediately, which effectively silenced them.

The scruff-hold method of transporting offspring is widespread amongst mongooses and results in the young curling up into the 'Tragstarre' posture (Zannier 1965). The effect of a scruff-hold was two-fold: firstly, it promoted a curling response which prevented the young from bumping over the ground, given the short forelimb length of the adult mongoose; secondly, it appeared to render the young helpless and inhibited struggling, which was essential for efficient transportation. Rasa (1985) showed that disturbed dwarf mongooses moved their young to a new and safer nest. It is likely that *Atilax* would act similarly, as illustrated by the mother transporting her young about the enclosure whenever disturbed.

Details of vocalizations are provided in Baker (1988). The attention call was exclusively a juvenile sound and showed structural affinity with the 'humph' call of adults. The main difference appeared to be in the marked frequency modulation of the attention call (Baker 1988). The last use of the attention call coincided with increased locomotory capabilities in hand-raised mongooses and probably signalled the ability of the young to remain near the mother by their own efforts. As this also coincided with weaning it is likely that the young begin to accompany the mother on short foraging trips at this age. Field data are required to substantiate this in naturally raised mongooses.

Weaning coincided closely with the eruption of the canines on day 29 and premolars on day 33 (Baker and Meester 1986). Continuation of suckling beyond the age of nutritional dependency on the mother may have helped to ensure that the bond formed between mother and young remained intact until the young were fully capable of survival on their own.

It was clear that young marsh mongooses had to learn how to deal with terrestrial prey, both through maternal guidance and experience. However, as soon as it was established that small moving objects were potential prey, mongooses were able to adapt their killing behaviour accordingly. Food envy appeared to play a role in encouraging the young to eat solids, and a maternal feeding growl stimulated attempts to retrieve prey from maternal possession. 'Hip-slamming' has been described by Rasa (1973a) in dwarf mongooses. In *Atilax* it developed around day 34, soon after the start of solid food intake, and appeared to contribute to the complex of behaviour patterns associated with food envy.

The fact that there is no significant difference in the onset of prey killing between naturally raised mongooses and hand-raised ones is not surprising as prey killing is an ability which develops with maturation of skills, such as speed of movement as well as ability to deliver a killing bite. In mongooses prey killing is most often a result of a bite directed at the crown of the head, such that the canine teeth inflict a fatal wound (Baker 1989; Rasa 1973a). Only when mongooses have reached a certain level of development will the killing bite be successfully administered. For this reason, perhaps, the attempt by naturally raised mongooses to kill prey at 102 days was unsuccessful. In the case of the crab kill by a hand-raised animal (K) at 129 days, the method of killing is different from that of

rodent capture. Marsh mongooses usually dispatch this prey by throwing it onto the ground (BAKER 1989).

In capturing aquatic prey the necessary techniques of 'feeling' and searching for submerged food appeared to be ones which required no learning in both naturally and hand-raised mongooses. From an early age the mongooses manipulated objects between the forefeet on the ground, almost as if unconsciously. The heightened sensory capacity of the feet and the associated elaboration of the neocortex in the brain (RADINSKY 1975) may account for the immediate competence of forefoot activity.

In general results show little difference in the rate of development of behaviour patterns in naturally-raised and hand-reared mongooses. However, pattern of development was different where maternal guidance was involved, such as in the development of prey killing patterns.

Detailed work on the postnatal behavioural development of herpestines is scarce. Table 3 summarises available information and shows close similarities in feeding patterns, locomotory development, grooming patterns and alarm responses amongst the six genera.

Table 3. **Postnatal behaviour development in herpestines**
Ages given in days

Character	*Mungos*	*H. ichneum.*	*Suricata*	*Helogale*	*Galerella*	*Atilax*
High-sit	16	60	23–33			42–53
Wean	19	32–64	30–63	35–40	49–63	29–40
Alarm	12		12		14–25	11–35
Fleaing				11–25	18	23–24
Egg break (hen)				75	203	52–130
Rodent kill			78	66	63	102–140
Play-biting	21			30		17–35
Anal drag	23			29–44		35–55
Cheek mark	40			24–39		60
Run well		28	21–40	24		26–35
Defaecate alone			22			29–39
Scratch			2			2
Lick well			30			36
Purring alone	present		present	present	present	absent ?grizzle

Sources: *Mungos* – ROOD (1975), VILJOEN (1980); *Herpestes ichneumon* – RENSCH and DÜCKER (1959), DÜCKER (1965), BEN-YAACOV and YOM-TOV (1983); *Suricata* – DÜCKER (1962, 1965), EWER (1963); *Helogale* – DÜCKER (1965), RASA (1973a, b, 1977, 1985), ROOD (1983); *Galerella* – JACOBSEN (1982); *Atilax* – BAKER (1987), present study.

Resemblance in the rate of postnatal physical development (BAKER and MEESTER 1986) is probably the underlying cause of this similarity, as development of certain behaviour patterns is clearly contingent upon development of locomotor abilities and visual ability, for example. The development of the alarm response is the clearest example of this, as vision is the faculty which releases this behaviour pattern. In *Atilax* eye-opening occurs around day 11 (BAKER and MEESTER 1986) and the alarm response develops on the same day. Eye-opening in *Mungos* begins on day 8 with alarm reactions developing on day 12 (VILJOEN 1980), while in *Suricata* eyes open around day 12 and the alarm response is shown on the same day (EWER 1963).

The development of the 'high-sit' (EWER 1963) or 'Männchenmachen' (DÜCKER 1962) showed some variation in maturation with social species developing the pattern earlier (Tab. 3). It seems likely that in the natural environment it would be more adaptive for the sociable species, such as *Mungos* and *Suricata*, which are also diurnal and which rely on

visual perception to detect predators, and probably also to maintain contact with conspecifics, to develop the 'high-sit' as early as possible in order that they are able to elevate themselves and extend their visual field. On the other hand, the solitary genera such as *Atilax* and *Herpestes ichneumon* tend to occur in more densely vegetated habitats, where visual predator detection is less important due to availability of continuous cover. In the case of *Atilax* this cover is extended by virtue of its nocturnal habit.

Manipulation and breaking open of hen's eggs varies quite markedly, with dwarf mongooses and marsh mongooses developing the ability earliest. Because all the herpestines appear to favour eggs little ecological significance can be attributed to the time at which this pattern develops in the different species, and it is more likely to be related to physical ability. RASA (1973a) notes that young *Helogale* are particularly voracious and for such a small animal to manipulate objects clearly requires considerable motivation and dexterity. In relation to head-body length, limb length in *Galerella* is shorter even than that of *Helogale* and this may account for the much delayed development in this genus.

In all herpestines the rapid development of locomotory abilities is clearly adaptive, in that it allows young to accompany their parents on foraging trips as soon as weaning commences, thus reducing parental responsibility as far as provisioning the young are concerned.

Development of scent-marking behaviour shows some variation. The sociable species (*Mungos* and *Helogale*) exhibit earlier development of both anal and cheek-marking, than the solitary *Atilax*, although slight overlap in anal marking development occurs between *Atilax* and *Helogale*. In order to promote integration into a sociable group it would be expected that early development of scent-marking methods would occur. As the anal mark is the 'identity mark' of the individual (RASA 1973b; GORMAN 1976; HEFETZ et al. 1984), it is not surprising that it develops early in sociable mongooses, where identification of all group members is desirable. In *Helogale*, however, it develops after cheek marking, which might be related to the handstand position which is adopted during anal scent deposition. It seems that this would be a more difficult task to perform than the simple anal drag produced by *Mungos* and *Atilax*, and so develops when locomotion and balance are coordinated. In *Atilax* the cohesiveness of the rearing group is not well developed, and so the early development of anal marking is essential to reinforce the short-lived rearing bond.

Purring has been recorded for most herpestines (Tab. 3). PETERS (1984) considers that vocalizations with a uniform structural pattern consisting of a rhythmical series of short, low-intensity sounds constitute close range friendly communication (including purring). In *Atilax* the only sound that falls into this category is the "grizzle" (BAKER 1988).

Despite the marked differences in rearing systems between solitary and sociable herpestines, the similarities in the development of postnatal behaviour patterns illustrates the overall cohesiveness of the group and provides few clues concerning phylogeny.

Zusammenfassung

Beobachtungen über die postnatale Verhaltensentwicklung von Sumpfmangusten (Atilax paludinosus)

Die mütterliche Pflege bei Sumpfmangusten wird beschrieben. Sie besteht aus Säugen, Reizen zum Harnen, Schutz und Lehren aller Geschicklichkeiten. Der Beginn von neun verschiedenen Verhaltenskategorien wird kontrolliert und beschrieben. Diese schlossen Lautgebung, Bewegungen, Putzen, Schreck, Geruchsmarkierung, Spiel und sexuelles sowie agonistisches Verhalten ein. Im Vergleich mit der nachgeburtlichen Verhaltensentwicklung anderer Vertreter der Herpestinen, zeigten Sumpfmangusten gewisse Ähnlichkeiten.

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Interpreting social behaviour of Wood bison using tail postures

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Abstract

Free ranging wood bison were observed to investigate the use of tail postures during social interactions. Our observations support the following conclusions: 1. Different tail postures were exhibited in different social contexts. Tail wagging was associated with grazing, while holding the tail horizontally or up were associated with aggression, sexual behaviour, and danger. 2. When bulls and cows were found together in groups, mostly cows raised their tails when disturbed by predators, while bulls raised their tail in sexual contexts. 3. In aggressive interactions between bulls, tail up was associated with dominance, tail wagging with submission. 4. The tail up posture was exhibited in more intensive situations than the horizontal tail posture, suggesting that the tail up posture was a graded form of the tail horizontal posture. 5. Individuals involved in play fights did not raise their tails, while at least one of two contestants raised the tail at the end of (but not during) escalated fights. We conclude that the recording of tail postures of bison can serve as an objective tool in the interpretation of bison social behaviour. The role of the tail posture as a possible signal in bison communication is discussed.

Introduction

Understanding social behaviour of animals requires the knowledge of the behavioural repertoire employed by animals in social interactions. For this reason a detailed account of body postures has been given, for example, for wolves (*Canis lupus*) and domestic cats (*Felis catus*) (Schenkel 1947; Leyhausen 1956). Tail postures in these species could be related to either dominance status, or state of emotions (level of fear or aggression). Hausfater (1977) presented a quantitative analysis of tail postures in baboons (*Papio cynocephalus*), in which he showed that tail posture correlated with age but not rank. Some studies on ungulates describe tail postures in addition to descriptions of body postures (Jarman 1979; Barrette 1977; Caro 1986).

Our observations of free-ranging wood bison (*Bison bison athabascae*) support the concern put forward by McHugh (1958) that bison behaviour patterns are often subtle and, therefore, difficult to determine objectively. Tail postures of bison have been often referred to in reports on bison social behaviour (McHugh 1958; Fuller 1960; Egerton 1962; Herrig and Haugen 1969; Lott 1974; Mahan 1978), suggesting that tail postures of bison might be indicative of either dominance status, level of aggression, or fear. In bison, strong development of hair on the head and neck region, and the large hump obscure objective descriptions of body postures such as the position of ears, stretching of the neck, and arching or stretching of the back. The tail, however, is a conspicuous body part and can be easily observed in relation to social behaviour.

In the above mentioned studies bison were observed to raise their tails to various degrees during aggressive, sexual, and alert behaviours, while they wagged their tails during grazing. However, no quantification or rigorous examinations of relationships were presented. Understanding the use of the tail in bison could be helpful in the interpretation of bison social behaviour. This paper describes the position of the tail of wood bison as a character feature in different social contexts.

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Materials and methods

The study was conducted on a free-ranging wood bison population in the Mackenzie Bison Sanctuary (MBS), Northwest Territories, Canada. There are no human settlements in the MBS, only one road leads through the area, and no fences restrict the movements of bison. During the time of this study, the population size was estimated at 2500 wood bison. The area used by the bison was approximately 10 000 km^2 (Gates and Larter 1990). The study was carried out from July 16 to August 16, 1990. The study area was Falaise Lake which was considered to be the core of the range of bison in the MBS (Gates and Larter 1990). Falaise Lake extends over approximately 60 km^2. It is a shallow lake consisting largely of open sedge (*Carex* spp.) meadows and willow (*Salix* spp.) savannah. The lake is surrounded by boreal forest.

Bison groups are highly fluid and associations among individuals are considered near random (Lott and Minta 1983; Vuren 1983). Observations on individuals marked with radio transmitters suggest that individuals range widely, using most of the area in and around the MBS. It is our impression that a major part of the individuals in the population spent some time on the study area during the data collection for the present study, and that the events sampled largely represent different individuals.

For behavioral observations, the minimum number of bison observed was three. When we spotted bison groups at a distance (usually > 150 m), we left the all terrain vehicles behind and approached the animals by foot. By hiding in the vegetation, we made an effort not to be detected by the animals. Bison which detected humans generally left the area immediately. Therefore, we believe that the behavioral data collected during this study was not affected by the presence of observers.

Binoculars and telescopes were used to observe the animals. Each observational session lasted one to three hours. We left the site after this time interval, in order to search for a new group of bison. This method was chosen in an attempt to maximize the number of different individuals observed. Approximately 80 h of observation were conducted by each of the authors and one additional observer. In addition to recording behaviour in the field, a video camera with a 12 × lens was used to record bison behaviour on VHS video tape.

Categories of behaviour

Seven categories of behaviour were noted: walk towards another individual; walk away from another individual; walk with another individual (includes parallel and one behind another); standing (animal standing with its head up); grazing (animal standing or walking with mouth in grass); lying; and flehmen (Herrig and Haugen 1969; Lott 1974).

Tail postures

Four categories of tail posture were recorded (Fig.): tail wagging (tail hanging down and whipped to either side at least every ten seconds; McHugh [1958] termed this posture "tail switching"); tail down (tail hanging down with no lateral movement); tail horizontal (proximal half of tail held horizontally; distal half of tail my or may not hang down); tail up (tail raised higher than 45° from horizontal). These tail postures were recorded when they were displayed for at least ten seconds. Transitory postures lasted less than ten seconds and were thus not recorded (for example, when lifting the tail from tail down to tail up, the tail was held for a brief moment at the horizontal position).

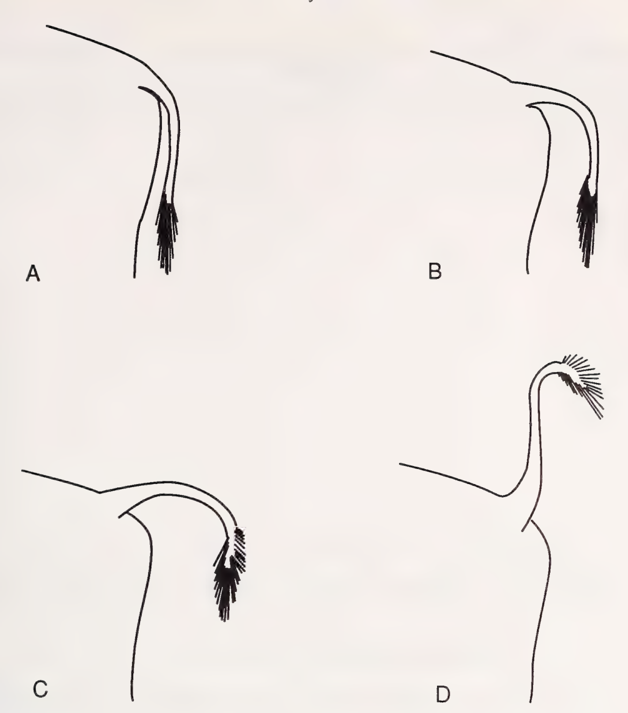
Context situations

Five context situations were recognized.

1. Grazing: The animal stood or walked with its head in the grass. Data on tail postures in the grazing context were collected from video tape. Each grazing animal was recorded on a data sheet once, when it and its tail posture could be first identified. Tape sequences were discarded, when there was a chance that individuals would be recorded a second time.

2. Alert: The animal stood with its head up and ears directed towards the source of danger. Bison groups disturbed by humans, were recorded on video tape. Each bison was recorded on a data sheet once, at the instant when it and its tail posture could be first identified. Because the different scenes of each group likely included the same individuals, the average frequency of bison adopting a given tail posture was calculated over the number of scenes. The averages from different groups were used as independent data points for statistical analysis.

3. Sexual context: A bull sniffed the genitals of a cow. Tail posture and category of behaviour were recorded for each of two interacting animals at the beginning and at the end of an interaction. An interaction started when one animal approached another to within two body lengths. This distance



Schematic representation of tail postures of wood bison. A: tail down; B and C: two forms of tail horizontal at the lower (B) and upper (C) margin of our definition (see text); D: tail up. Tail wagging was similar to tail down, except with lateral movements

was an arbitrary measure. The end was marked when one animal moved away from the other or when at least one animal changed its behaviour. Although some events were recorded in the same groups of bison, we assume that different individuals contributed to our observations. This assumption is based on the large number of individuals in groups, and the frequent changes of individuals between groups (KOMERS, unpubl. data). Tail postures of bison during sexual contexts were also recorded on video tape. For each interaction in which the bull showed tail up, his tail posture was also noted, by rewinding the tape, when he was more than two body lengths from the cow.

4. Aggression: An aggressive interaction was defined as one bull approaching another to within two body lengths and, subsequently, one of the two bulls turning away using at least two steps. The individual that turned away was considered the loser. This definition included subtle forms of interactions as well as escalated fights. Data were collected and analyzed in the same way as under "sexual context", except that instead of a cow, a bull was approached by another bull.

5. Locking horns: Two animals of any sex and age class standing head to head with horns touching when the interaction was first recorded. If an aggressive interaction resulted in a fight and, therefore, the two animals locked horns, the locking horn behaviour was considered part of an aggressive interaction and consequently not recorded under 5. Category 5 was established because some interactions were only noticed at the time when two animals locked horns.

When video tape recordings were used for data collection, the same criteria for behaviour and tail postures were applied, as for observations in the field. The tape was not played back in slow motion to make behaviours or tail postures more obvious.

Results

Tail postures in different contexts

On average, 97.3 % ± 7.0 % (SD) of grazing animals were tail wagging. Of the 115 animals sampled, two held their tail horizontally, and four showed tail down. No animal was grazing with its tail up.

Table 1. **Tail postures of wood bison displayed in different contexts at the start and at the end of an interaction**

The numbers represent all animals involved, including both interacting partners

Tail Posture	Aggression	Behavioural context Locking horns	Sexual
Start			
Up	10	1	19
Horizontal	8	0	6
Down	7	0	11
Wagging	7	17	7
End			
Up	10	2	17
Horizontal	3	1	5
Down	4	1	12
Wagging	15	14	6

Tail posture varied in different context situations (Tab. 1: start of interactions, $\chi^2 = 40.4$, df = 6, $p < 0.001$; end of interactions: $\chi^2 = 24.8$, df = 6, $p < 0.001$). Both at the start and at the end of interactions, tail wagging was most often displayed in the locking horns context, while tail up was used more often in aggressive and sexual contexts (Tab. 1).

During alert behaviour, the average frequencies of the four tail postures observed were significantly different (up: 3.7; horizontal: 1.6; down: 3.2; wagging: 0.3; averaged over three groups with three video sequences each), indicating that tail up was observed most, and tail wagging least frequently (Kruskal-Wallis test with χ^2-approximation, $\chi^2 = 8.08$, df = 3, $p = 0.044$).

Table 2. **Tail postures of wood bison bulls and cows during sexual context**

The numbers represent all animals involved, including both interacting partners

	Tail posture Up	Horizontal	Down	Wagging
Bulls	16	2	0	3
Cows	1	3	12	4

In sexual contexts, bulls that sniffed the genitals of cows exhibited tail up most frequently, while females exhibited tail down most often (Tab. 2, Fisher exact, $p < 0.001$). Note that females exhibited tail down more often than tail wagging. Conceivably, tail wagging would interfere with the investigative behaviour of bulls.

Also in the sexual context, tail up was mostly associated with walk towards, while tail down and horizontal were associated with standing and grazing at the start of interactions (Tab. 3, Fisher exact, $p < 0.001$). At the end of interactions tail up was mostly associated with flehmen, while tail down and wagging mostly with standing and grazing (Tab. 3, Fisher exact, $p < 0.001$). Because sex probably influenced tail posture and behaviour, a two-way analysis of the contingency table would have been appropriate. However, small cell frequencies did not allow for such an analysis.

Tail posture as indicator of dominance

Only 6 of the 16 pairs of aggressively interacting bulls contained at least one of the contestants with a wagging tail at the start of the interaction, compared to 13 of 16 pairs at the end ($\chi^2 = 6.3$, df = 1, n = 32, $p = 0.012$). This suggests that one of the two bulls changed his tail posture to wagging during the interaction.

Independently of the above results, we recorded the winners, losers and the tail postures in 23 interactions for which the tail could be observed only at the end. Winners had their tails either up (21) or down (2), while losers had their tail either down (14) or

Table 3. **Tail postures of wood bison at the start and at the end of sexual interactions**
The numbers in parentheses represent tail postures for males only. The difference between the sample sizes at the start and end was because some tails were out of sight at the end of the interaction

Tail posture	Behavioural category		
Start			
	Walk towards	Stand	Graze
Up	19 (19)	0	0
Horizontal	2 (2)	3 (0)	1 (0)
Down	0	5 (0)	6 (0)
Wagging	1 (1)	5 (0)	1 (0)
End			
	Stand	Graze	Flehmen
Up	1 (0)	0	15 (15)
Horizontal	2 (0)	0	3 (3)
Down	7 (0)	5 (0)	0
Wagging	2 (1)	1 (1)	3 (3)

wagging (8) (Fisher exact, $p < 0.001$). Tail horizontal was not observed. This suggests that dominant bulls exhibit tail up, while submissive bulls exhibit tail wagging.

Tail as an indicator of intensity

We assumed that the distance between an actor and an interacting partner is equivalent to the intensity of a possible stimulus on the actor (MANNING 1979; Alcock 1989). If true, and if tail up reflects a stronger reaction than tail horizontal, then one would expect that animals further away from their interacting partners would exhibit tail horizontal more often than tail up. Alternatively, bulls that are aggressive could remain with tail up for extended periods of time, irrespective of the proximity of interacting partners.

Bulls were recorded with their tails up within two body lengths of a cow (sexual context) in nine video sequences. When they were further than two body lengths, either before or after approaching and sniffing, they showed tail horizontal in eight and tail up in one instances (binomial two-tailed test, $p = 0.02$).

Bulls were recorded with their tails up within two body lengths of a bull (aggressive context) in nine video sequences. When they were further than two body lengths, either before or after approaching, they showed tail horizontal in eight, and tail up in one instances (binomial two-tailed test, $p = 0.02$).

We conclude that the tail up posture was exhibited in more intensive situations than the tail horizontal posture. This response suggests that tail up was a graded form of tail horizontal.

Play fights and escalated fights

Nine fights among mature bulls were recorded on video tape. In all cases, bulls wagged their tail during the fight. In seven of the nine cases, one of the contestants exhibited tail up at the end of the fight. Thus, the tail was raised significantly more often at the end than during a fight (Fisher's exact, $df = 1$, $p = 0.002$). This observation suggests that in order to distinguish play fights (termed "play battles" by McHUGH 1958) from escalated fights, the position of the tail should be noted at the end of an interaction, and not while the animals lock horns.

This conclusion is further supported by results presented in Table 1. Both individuals exhibiting tail up under the locking horns context were mature bulls interacting with other mature bulls. The other individuals recorded in this context included three pairs of

subadult bulls, three pairs of yearlings, and one pair of calves. Presumably, immature bison fight for training their motor skills as opposed to competing for resources Rothstein and Griswold 1991). Indeed, in only one of the cases involving immature bison, interacting partners walked away from each other. The others either remained standing together or walked away together. In both cases in which one of the bulls raised his tail, the two contestants walked away from each other.

Discussion

When bison in our study did not interact in a way that could be detected by the observers, then they were mostly wagging their tails. This suggests that tail wagging was a neutral tail posture, thus it was exhibited when no social stimulus was present (Hausfater 1977). However, tail wagging is presumably used by herbivores to repel biting insects. The impact of biting insects on the behaviour of wood bison can be substantial (Melton et al. 1989). We did not observe wood bison during insect free seasons. It is conceivable, that bison do not wag tail during the winter. If true, we suspect that they keep their tails down as a neutral position.

Tail horizontal and up was associated with aggression, sexual behaviour, and danger. Thus, the same tail posture was associated with different behaviours in different contexts. This could potantially make the interpretation of tail postures difficult. We point out, however, that when recording tail postures of bison, it is important to know the behavioural context and the sex of the animal. We feel that this requirement is easily met by an observer, because the behaviour for each animal under observation and that of the surrounding animals is usually known for a period of a least a few seconds.

The above consideration is further illustrated by tail postures not examined in our study. For example, cows can exhibit tail horizontal or tail up after copulation. The tail posture of cows in such a situation may last for one to several hours (McHugh 1958; Herrig and Haugen 1969; Berger 1989). Tail up is also exhibited during defecation (Herrig and Haugen 1969). The contexts of such tail postures are unmistakable.

We agree with McHugh (1958) and Rothstein and Griswold (1991) that discriminating between playful and agonistic interactions in the wild is often difficult without relying on subjective interpretation. Our results suggest that bison did not raise their tail in a playful context, while they did so at the end of aggressive interactions. Moreover, the intensity of an interaction seemed to be indicated by the height to which the tail was raised.

Tail up in the alert context seemed to be associated with irritation (McHugh 1958). While we presented data on bison reacting to human disturbance, we also observed that bison reacted similarly to the disturbance by wolves.

Results presented in this study support the concept that the tail in bison may be employed in visual communication. We do not claim, however, that the evidence is conclusive. A rigorous investigation of behavioural relationships among bison receiving a signal and bison sending a signal is required. Our results suggest that tail postures of bison can serve as an objective tool in the interpretation of bison social behaviour. In fact, in many studies describing social behaviour of animals and the corresponding body postures, the tail was part of the description (Schenkel 1947; Leyhausen 1956; Walther 1958; Jarman 1979; Barrette 1977; Caro 1986). Conceivably, the tail could be used in species other than bison as an easily observable, objective tool to describe and interpret behaviour.

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Zusammenfassung

Das Interpretieren sozialen Verhaltens von Waldbisons anhand von Schwanzhaltungen

Freilebende Waldbisons wurden beobachtet, um die Schwanzhaltungen während sozialer Interaktionen zu studieren. Unsere Beobachtungen lassen auf die nachstehenden Folgerungen schließen: 1. Unterschiedliche Schwanzhaltungen wurden in unterschiedlichen sozialen Zusammenhängen gezeigt. Schwanzwedeln hing mit Grasen zusammen, während ein waagrecht angehobener und ein aufrechter Schwanz sowohl mit aggressivem und sexuellem Verhalten, als auch mit Gefahr in Zusammenhang gebracht werden konnten. 2. Wenn Kühe und Bullen sich gemeinsam in einer Gruppe aufhielten, zeigten Kühe einen aufrechten Schwanz in Gefahrensituationen und Bullen während sexuellen Verhaltens. 3. Während aggressiver Interaktionen zwischen Bullen hingen ein aufrechter Schwanz mit dominantem Verhalten und Schwanzwedeln mit subdominantem Verhalten zusammen. 4. Ein aufrechter Schwanz wurde in extremeren Situationen gezeigt als ein waagrecht angehobener Schwanz. Also war ein waagrecht angehobener Schwanz eine gemäßigte Form von einem aufrechten Schwanz. 5. In Spielkämpfen zeigten Bisons keinen aufrechten Schwanz, während bei ernsthaften Kämpfen zumindest einer der Kämpfenden am Ende des Kampfes einen aufrechten Schwanz zeigte. Das Beobachten von Schwanzhaltungen kann als ein objektives Mittel zur Interpretation des Sozialverhaltens von Bisons dienen. Die mögliche Rolle von Schwanzhaltungen in der Kommunikation von Bisons wird diskutiert.

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Social environment of Isard kids, *Rupicapra pyrenaica p.*, during their ontogeny

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Abstract

Investigated the monthly social environment of cohorts of young isards, *Rupicapra pyrenaica p.* during one and a half years, in an attempt to understand some aspects of their socialization process. We postulate that the sociality of adults is greatly influenced by their ontogeny. The composition, in age-sex classes, of 2,001 groups observed in open mountainous environment is described. During their childhood, young isards go through high sociality periods, during which they are in contact with many and various conspecifics. During other periods, they are in closer association with females only. Both association patterns may play a role in the socialization process. Contact with males is less frequent and occurs for the first time during the rutting period. The most drastic changes in the social environment of the young occur with the arrival of the new generation of kids. The high sociality period of spring is a rather sensitive period during which social associations are very diversified, and social networks may be reshaped. The role of ontogenetic experience in formation of social associations is discussed.

Introduction

The social structure of wild ungulates has been the subject of many studies. Comparisons of data concerning various populations of a given species under different ecological conditions have often indicated intraspecific variations in social systems (Lott 1983). This suggests that a species do not have a fixed specific social organization or structure, but that both vary greatly under different environmental conditions (Hirth 1977; Schaal 1982; Lott 1983; Alados 1985; Maublanc et al. 1987). According to Lott, this would make developmental questions more salient. Berger (1979b) noted from reviews describing adult spacing patterns that only few authors considered the process itself, i.e., the ontogeny of social behaviour. He stated that, in Bighorn sheep *Ovis canadensis,* social behaviour and subsequent spatial associations of lambs were influenced by the size of groups within which they were reared (Berger 1979a, b).

An individual exhibits a social predisposition depending on its sex, age and social experience during its ontogeny, within the limits of specific characteristics (Mason 1978). This social tendency develops in a social and physical context, in constant dialectic interaction with it. Each new generation modifies all existing relations in a group, and receives the influence of the whole group as feedback (Bon and Campan 1989). An individual goes through an "ontogenetic trajectory" (Mason 1978; Wiley 1981; Bon and Campan 1989), shaped both through internal and external constraints.

This study is based on the assumption that the social context is the framework in which behaviour develops and thus that shapes it into that of the full adult. The sociality of the isard is thus dealt with through a developmental approach. The results are presented in terms of kids' social environment, which is a more "animal centered" approach than a mere description of the social structure in different group types or sizes. Moreover, the information presented may provide the basis for future comparative investigations in isards.

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Materials and methods

Observations were made in the National Wildlife Reservation of Orlu, in the Pyrénées Mountains, France. In this area, the isard, *Rupicapra pyrenaica pyrenaica,* a species close to the chamois *Rupicapra rupicapra,* but now considered as distinct (Nascetti et al. 1985; Masini and Lovari 1988) has been protected since 1943. The population reached a high density of about 30 animals/100 ha based on annual counts made by the National Game Agency, responsible for the management of the reservation. Most of the observations were made on about half of the protected area, which covers 4,265 ha. The altitude ranged from 1,400 m in this valley, up to 2,765 m for the highest summit. Vegetation consisted mainly of meadows in the valleys, beech forest with *Fagus sylvatica* up to 2,000 m, some mountain pine forest, *Pinus uncinata,* and alpine pasture above.

Data were collected from May 1989 to December 1990. A "group", at any given time, was distinguished from a neighbouring one when the distance between them was greater than the average inter-individual distance within the group (Clutton-Brock et al. 1982). Under field conditions, this generally corresponded to intergroup distances of 50 m or more (Berducou and Bousses 1985; Richard and Menaut 1989; Richard and Pépin 1990). All visible groups observed on wide panoramas from fixed observation points were recorded throughout the day. Hence, the data only concern observations in open habitats in which visibility was sufficient. Groups were described by their location on an aerial photograph and by the number and nature of their components. 15,179 animals in 2,001 groups of known composition were recorded (9.2 % males, 43.3 % females, 47.5 % young). In this study we generally referred to "mixed groups" as associations containing males, females and young, and to "matriarchial groups" as ones without males.

This work describes the monthly social environments of cohorts of young born in the same year. The field work was conducted over a period of 1.5 years, so the young born in 1988 were observed at the age of 1 to 2.5 years, those born in 1989 from birth up to 1.5 years, and the 1990-generation from birth up to 7 months. Ages were estimated in months as all births were relatively synchronous.

Since the study was centered on the ontogeny of associations of young animals, no strict classification was used to separate them artificially into pre-determined classes. The customary classification of animals as kids, yearlings and subadults did not suit this study, because it created artificial gaps in calculating proportions of various classes at the very sensitive period of parturition. Such artifacts would hide the behavioural events occurring during the same time.

To describe the social environment from the "young's point of view", the young were named with reference to a focal cohort Y. Thus, Y+1 refers to the previous generation (young 1 year older than the focal ones), Y+2 refers to animals 2 years older, Y−1 to the succeeding generation, (1 year younger) and Y−2 to animals two-years younger.

For the sake of clarity, we use "kid" to refer broadly to less than one-year-old young, "yearling" for one- to two-year-old young, and the general term "young" for animals less than 2.5 years old. "Elders" refers to non-adult animals older than the individual in question.

As it is very difficult to determine the ages of adult isards (because of the poorly defined annual horn growth and the large inter-individual variations) individuals of 2.5 years of age or more were simply separated into sex classes: adult female (F) and adult male (M).

The results are presented as percentages of animals of each age class involved in various types of associations. This accurately represents the real distribution of animals in different groups, and thus their social experience, better than the commonly used system enumerating the proportions of groups encountered, which does not take into account group size (Barrette 1991). The sizes of different associations are described here by the "Typical Group Size", calculated using Jarman's (1974) formula:

$$TGS = \frac{\sum_{i=1}^{n} (G_i)^2}{\sum_{i=1}^{n} (G_i)}$$

where G_i is the group size of each of the i groups considered. Typical Group Size is also a more animal-centered estimation, representing the group size experienced by the majority of animals, in other words by the "average individual". This value is especially suitable for species that form many small groups and few large ones (Hillman 1987), or for species in which groups are very fluid (Barrette 1991). Actually, both these conditions were present in our population.

Since our data concern individuals distributed in various group types, the samples are distributed nonuniformly, and are not independent (when several kids are in the same group, they are not independently distributed). Statistical analysis was not attempted in our study for the same reason as that stated by Festa-Bianchet (1986) and since sample sizes were sufficient to make the figures for variations of proportion reliable.

Results

Social associations of young up to 1.5 years of age

Monthly variations of the young/female ratio is presented in Figure 1, showing that the period of parturition was very short. The first kids were observed on the 20th of May, 1989 and almost all of them were born by the beginning of June. The ratio kids/females seemed to be rather stable during the first year.

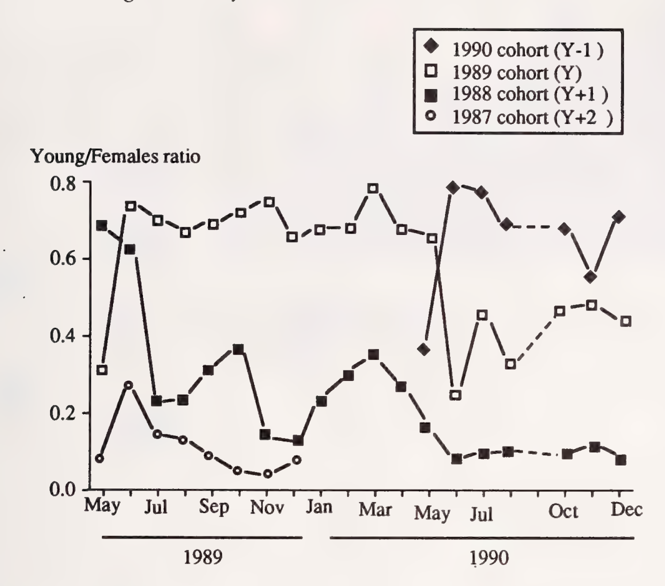


Fig. 1. Young/female ratio for 4 temporary cohorts of young, during 1.5 annual cycles

During their first 7–8 months of life, kids were mostly observed associated with females only, or with females and elders (Fig. 2a). Exclusive association of kids with females decreased during summer, and increased slightly again at the beginning of winter (Fig. 2a, c). Two categories of elders were distinguished for 1990 (Fig. 2c), indicating that kids were in contact earlier with one-year-old animals (June), rather than with the two-year-olds. From May to December, only about 10 % of the kids were not in groups containing peers. These occurrences corresponded to isolated mother-kid dyads, or, to a lesser extent, to mother-kid-yearling trios.

Females were always present in the kids' social environment. Young kids (up to 9 months old) were never observed without the presence of at least one female (Fig. 2b). The presence of kids in mixed groups, with at least one male, increased steadily during the summer and the autumn. This was particularly obvious during the second study-year (Fig. 2c). In November (Fig. 2b), at the peak of the rutting period, the frequency of observations of kids in mixed groups reached its maximum (44 %).

In the winter (January-February) eight-to-nine-month-old kids were involved mainly in complex associations: 48 % with older young (Y+1) and females, 32 % within mixed groups (Fig. 2) and the remaining 20 % were with females only.

The following March, when they were ten months old, more than half of the young were again associated with females only. This increase may be related to the peak of the young/female ratio in March (Fig. 1). Spring was also marked by a second rise of frequentation of mixed groups in April and by the emergence of associations with other young and/or males without any female. It reached its maximum in May (Fig. 2b).

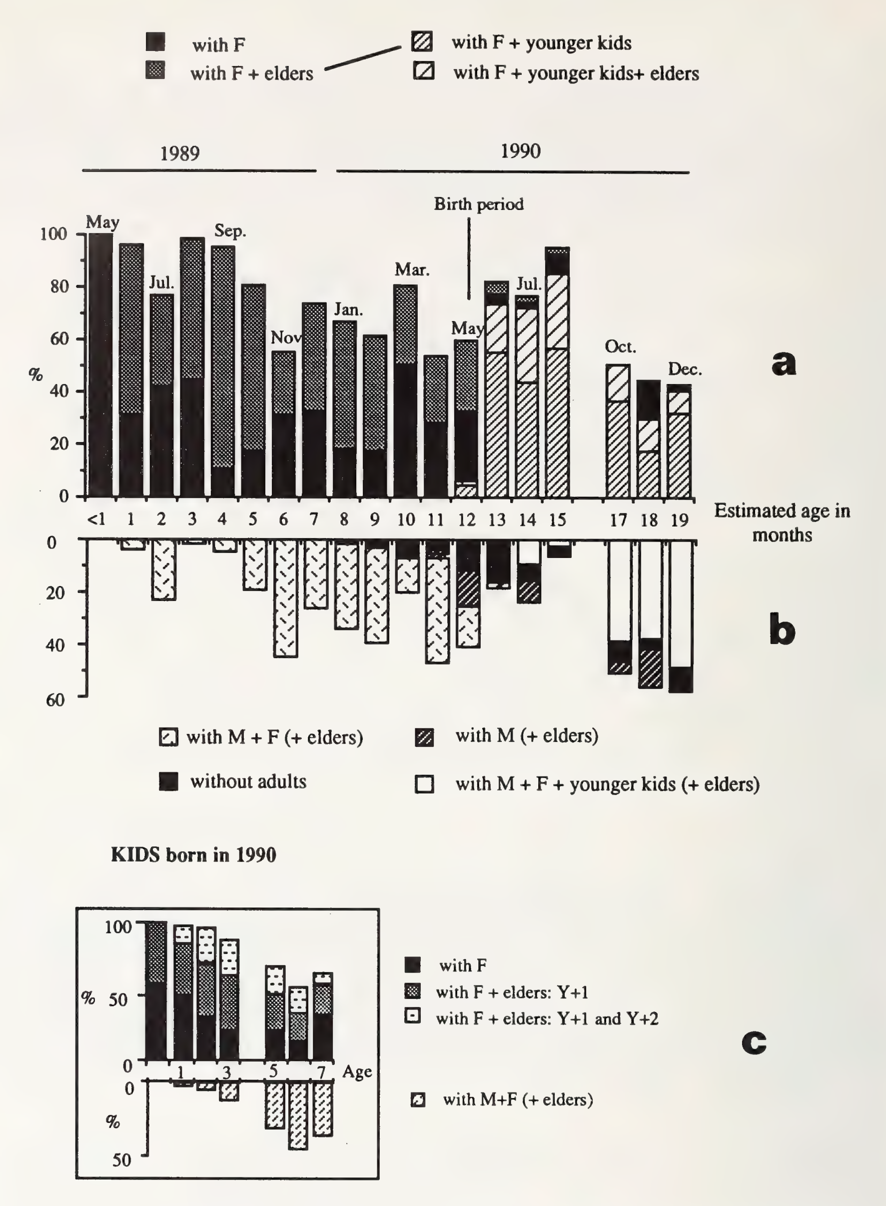


Fig. 2. Patterns of association of young between birth (in 1989) and 1.5 years of age. a: associations without males; b: association with at least one male or without adults; c: young born in 1990

The most noticeable irregularity in these smooth seasonal variations occurred in May, when the mothers left their offspring and isolated themselves to give birth. At that time, the young/female ratio dropped abruptly (Fig. 1). This reflects the sudden break off the exclusive bond between young and mother. During this period, the young presented the largest diversity in their associative tendencies: 14 % with peers and males, 27 % alone with females, 26 % in matriarchial groups and 12 % in mixed groups (Figs. 2, 3). It is of interest to note that, as observed during the first 8 months, about 10 % of the kids were not in contact with peers in groups.

In June 1990, while almost all females had given birth, all the yearlings massively joined females with their newborn kids (Fig. 2a), and also some elders as we already observed in the previous May (1989). Note that before and after birth, these two kinds of groups (young with F, Y+1, Y+2 as well as young with F, Y−1, Y+1) were both composed of females and three generations of young. However, for the focal kids, social environment was quite distinct since, in the first case, they stayed only with elders, whereas in the second case, they were with elders and younger, and had lost the primacy of the bond with the mother.

The young/female ratio increased again in July 1990 (or even later in 1989), but some yearlings probably became dispersed, since this ratio never regained the previous level (Fig. 1). The association of one-year-old young with females and new-born kids (Y−1) was predominant during Summer 1990; only a few stayed apart from the females, and were associated with siblings and males. Although we could not always confirm their sex, we feel the majority of the latter group were young males.

Social associations of young between 1.5 and 2.5 years of age

Figure 3 shows the generation of young born in 1988. One-year-olds (in Summer 1989, Fig. 3a) were more often associated with elders (Y+1) in matriarchial units (52 % in

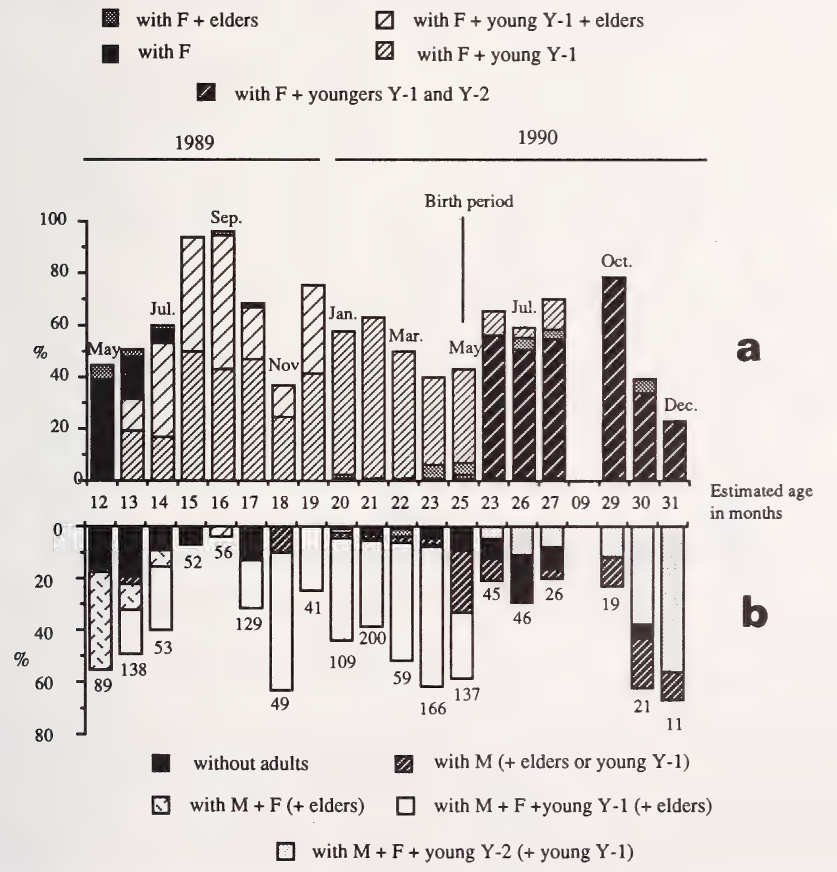


Fig. 3. Patterns of association of young (born in 1988) between 1 and 2.5 years of age. a: association without males; b: association with at least one male or without adults

September 1989) than the one-year-old young observed in the following summer (29 % in August 1990, Fig. 2a).

In November 1989, at the peak of the rutting season, 53 % of the yearlings were observed in mixed herds, while 36% were in matriarchial ones. They were in reversed proportions compared to the months before and after. In 1990, yearlings born in 1989 were observed in mixed herds from October to December (Fig. 2b).

In the winter, most of the 20-month-old young were still involved in matriarchial or mixed units until the next breeding season, while the 25-month olds once more tended to associate with peers or with males (Fig. 3). Later, they were observed mainly in matriarchial groups, and again joined mixed associations that were formed in November.

Associative tendencies of adult females

As grouping with females is very important in the social environment of the kids, it is of interest to note that association of females with males occurred mainly between October and April (Fig. 4). These mixed associations, with several generations of young, corresponded, most of the time, to large gatherings in favourable grazing areas. These were the largest type of association and reached a maximum in April and in November 1990 (Table 1). During the summer, the sexes were separated, (with a brief exception in July 1989), and most of the females were observed in matriarchial groups. About 15 % became isolated or formed small all-female units in the breeding period (May).

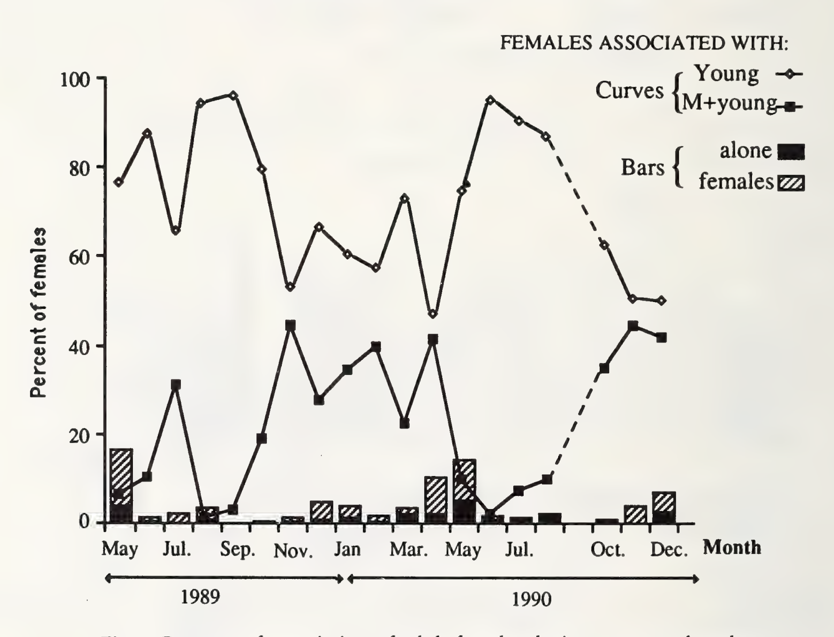


Fig. 4. Patterns of association of adult females during 1.5 annual cycles

The frequency of female associations with kids only decreased from parturition and during the rearing period, but reached a new peak in March. During the summer, females with newborn kids progressively frequented groups of increasing social complexity.

Typical Group Size of female-kid groups reached its maximum just after parturition (Tab. 1): about 15 in May 1989, and 27–33 in May-June 1990. It then sharply decreased during the summer (about 4 in August or September).

Matriarchial associations (containing at least 2 generations of young: FY), were largest

Table 1. **Typical Group Size (TGS) and mean group size (mgs) of the various associations**

		Year 1989								Year 1990											
		May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
ALL	TSG	42	26	18	22	32	23	43	65	40	40	54	79	48	33	25	28	–	24	36	8
	mgs	*7*	*7*	*8*	*7*	*16*	*10*	*13*	*13*	*13*	*12*	*11*	*20*	*12*	*11*	*9*	*10*	–	*10*	*14*	*4*
MFY	TGS	20	28	28	–	18	22	44	19	29	55	24	94	72	19	30	19	–	41	55	12
	mgs	*31*	*21*	*20*	–	*52*	*16*	*32*	*13*	*19*	*28*	*19*	*61*	*40*	*17*	*16*	*18*	–	*34*	*34*	*10*
MM	TGS	16	2	–	2	–	5	3	2	2	3	7	10	10	7	12	–	–	6	5	2
	mgs	*8*	*2*	–	*2*	–	*4*	*3*	*2*	*2*	*3*	*6*	*7*	*6*	*8*	*6*	–	–	*3*	*4*	*2*
MY	TGS	13	5	–	–	–	–	2	2	2	8	2	16	16	7	23	3	–	11	16	4
	mgs	*10*	*5*	–	–	–	–	*3*	*2*	*2*	*6*	*2*	*13*	*12*	*6*	*12*	*3*	–	*8*	*10*	*4*
YY	TSG	6	5	3	2	–	3	–	1	3	5	3	2	4	3	2	1	–	2	1	2
	mgs	*6*	*3*	*3*	*2*	–	*3*	–	*1*	*2*	*4*	*2*	*2*	*3*	*2*	*2*	*1*	–	*2*	*1*	*2*
FK	TGS	15	7	7	6	4	5	9	8	10	9	7	6	27	33	8	4	–	5	6	3
	mgs	*14*	*4*	*5*	*5*	*3*	*4*	*6*	*5*	*5*	*5*	*5*	*4*	*15*	*8*	*5*	*3*	–	*4*	*4*	*3*
FY	TSG	7	41	12	25	24	17	22	24	27	20	10	12	30	30	18	18	–	13	16	9
	mgs	*7*	*13*	*9*	*11*	*16*	*11*	*12*	*13*	*15*	*13*	*9*	*10*	*16*	*16*	*12*	*13*	–	*8*	*13*	*6*

ALL = groups with all categories of individuals; MFY = groups including male(s), female(s) and young; MM = male groups; MY = groups including male(s) and young; YY = groups of young; FK = female(s)-kid(s) groups; FY = females with at least 2 generations of young.

in June 1989 (TGS = 40), and in May-June 1990 (TGS = 30; Tab. 1). During Summer 1989, although the most of the kids, yearlings and females were in this type of herd, these groups were scattered in small units.

Associative tendencies of adult males

As males were part of the social environment of kids and young at least at some periods of the year, it is of interest to look at the associative tendencies of the males themselves. During the year, on average, about 33 % of the adult males grouped together and up to 87 % if we consider that the male-young associations observed in May concern mainly young males. The relative proportion of these all-male associations reached its minimum in winter (16 % in December 1989 and in November 1990). Around 10–30% of the males were observed alone, others in mixed associations with females and young, mostly during Winter 1989 and Autumn 1990.

The size of male-male associations reached its highest peak in April-May, as did male-young and young associations. However, this type of group was not more frequent at this period, only the number of animals per group was higher (up to 22 adult males).

Discussion

Following the social environment of the kids of *Rupicapra pyrenaica,* one can project the presence of a pattern similar to that proposed by Bon and Campan (1989) for moufflons, and trace a "standard ontogenetic social trajectory" of an "average individual". Each step of such a trajectory as well as the variations of the social environment along the yearly life cycle, may be influenced by either biological or ecological factors.

Isolation for parturition is a well known phenomenon, described in most ungulate species, wild or domestic (Lent 1974). It allows the establishment of an exclusive bond between mother and newborn, each learning to recognize the other individual (Lent 1974; Lickliter and Heron 1984; Poindron et al. 1984). Mother-kid association is generally considered to be the basis of ungulate sociality, and often as the only stable entity (Bouissou and Hövels 1976; Gonzalez and Berducou 1985; Bon et al. 1986). In "follower" species, kids stay close to the mother during their first weeks of life, and accordingly are found together within the same groups (Epsmark 1971; Lent 1974). Social environments of kids initially seem to depend mainly on those of their mothers.

After parturition, in our population of isard, mothers gather together in large flocks (up to 40 females) in open areas, each one followed by her kid. The kid/female ratio is usually 1 in such groups. Ferrari et al. (1988) related these matriarchial groupings in the Appenine chamois *Rupicapra pyrenaica ornata* to the particular diet of females during lactation and early weaning of kids. On the other hand, Hillman (1987) thought that, in the common eland *Tragelaphus oryx* aggregations of females with young might be due to the active gathering of the calves, which were physically attracted to one another. In this case, the females follow their offspring into those gatherings. In our study, although kids seem to follow primarily their mothers, they also have a great attraction for peers, which might play a role in the formation of the post-breeding nursery groups. These associations were actually the first occasion of high social interactions in the kids' experience, and the kids often strayed away from their mothers and had many contacts with peers and engaged in long sequences of play involving most of them (Richard-Hansen 1992b). Additional yearlings joined these associations, staying more or less peripheral, and providing new social partners for the kids and a progressive enrichment of the social context. These large flocks seemed to include, for a short time, most of the females, who usually and independently frequented partly overlapping home ranges, as demonstrated by following some marked animals (Richard-Hansen, unpubl. data). However, differences may exist in the social environment of the kids. In the Ossau population (another area of the Pyrénées) Berducou and Bousses (1985) observed 1/5 of isard kids in mixed herds as early as June.

In our observations, the large nursery flock did not last more than 1–2 weeks (end of May-beginning of June) after which most of the animals moved up to summer ranges. We suspect that they moved to the higher altitudes to find more rocky areas, to avoid heat, direct sunshine or insect harassment, as well as pressure from domestic animals that range on alpine meadows.

In the summer home ranges, the groups were smaller during mid-day and in many instances were reduced to mother-kid or mother-kid-yearling units, the animals spending these hot hours lying down in narrow shaded shelters, behind rocks (Pépin et al. 1991). Larger herds of isards occurred in the morning and in the evening, when the small units, hardly observable during the day, gathered to graze on prairies (Pépin et al. 1991). Males were seen to join these flocks for short periods, especially in the highly attractive zones, where salt-licks were laid out for domestic sheep and cows (Hansen et al. 1992; Ingold and Marbacher 1991). Similar observations of smaller group sizes of moufflons in the summer were made by Bon and Campan (1989). These authors proposed that the small group sizes were formed in response to high temperatures and impoverishment of the

meadows. It is of interest to note, however, that other studies on the chamois (Elsner-Schack 1985; Krämer 1969) or Appenine chamois (Lovari and Cosentino 1986) have shown the opposite to be true, maximum group size being attained in summer.

Isards came back to their previous home range during September, which seemed to be a transitory period. Latter on, during the rutting period, many kids were included in large flocks gathered on prairies. Males, actively looking for mates, were then running from one group to the other and temporarily becoming part of them. Once more, we may note differences between distinct areas: while 80 % of the females belonged to mixed associations in Ossau in November (Berducou and Bousses 1985), less than 50 % did in Orlu. This difference can be related to the higher proportion of mixed groups in the Ossau population. Thus, in our study as in the Carlit population (a further area of the Pyrénées, Gonzalez and Berducou 1985), kids were in sustained contact with males for the first time in their lives in November, i.e. during the rutting season. Bon and Campan (1989) also noted that 7–8 months-old moufflon lambs *Ovis ammon musimon* joined mixed groups, following their mothers, in the rutting season. During winter, the animals were usually found at higher altitudes (about 2,000 m) where cliffs, high slopes and windy ridges reduce the thickness of snow. Thus it appears that the causes of this move, like that in summer, are mainly environmental factors. Actually, when there was no snow, as occurred during the Winter of 1989–1990, most animals continued to frequent the pastures.

In March, as they approached one year of age, the young went through a period of reinforcement of exclusive association with females, as shown by the increase in the percentage of this type of association, and of the young/female ratio. We already suggested in a previous study (Richard and Pépin 1990) that kids could go through regressive periods in their development, during which they stayed closer to females and spatially more central within the groups, as observed for 1–2 month-old kids. This may have important implications in the social system by its possible causal value explaining the formation of matriarchial associations of females and daughters as suggested by Horwitch (1977) for the ibex. This hypothesis still has to be confirmed by estimation of mother-kid distances and kid's behaviour. Lovari (pers. comm.) also suggested that Appenine chamois in Abruzzo *Rupicapra pyrenaica ornata* may form matriarchial units in which daughters stay with their mothers. Furthermore, one marked mother-daughter dyad in our study area remained closely associated for over two years (Richard-Hansen 1992a), until they were broken up by accidental death.

April was another period of high sociality with formation of very large herds on the lower prairies, where the grass grows first. These aggregations, certainly due to feeding opportunities, were also the occasion of intense social contact between yearlings, gathering into subgroups of peers, leading to the groups of young observed in April and May. Some males were also present in these gatherings, integrated or in separate male groups, and some yearlings were observed to follow them very closely and appeared to be integrated into the groups, as shown by emergence of "MY" associations. In the Ammergauer Mountains, Bavaria (Elsner-Schack 1985), seasonal factors had inverse consequences: in this area, smallest group sizes were observed in spring and autumn, due to scattered food sources.

During the parturition period, in May, we observed many associations of young, as more and more females isolated themselves. Most authors state that these juvenile associations exist during parturition or during summer, in various ungulate species: isard (Gonzalez and Berducou 1984; Berducou and Bousses 1985), Spanish ibex (Alados 1985), white-tailed deer (Hirth 1977), Siberian ibex (Horwitch et al. 1977), moufflon (Gonzalez and Berducou 1985; Bon and Campan 1989), reindeer (Epsmark 1971), and red deer (Clutton-Brock et al. 1982). The wide variety of social environments of young described in this study at this transitory period of parturition reflects the instability of their

Table 2. **Overall view of social and physical environments experienced by kids during their ontogeny**

Period	Age in months	Biological event	Type of association	Physical environment
May	0	Birth	Mother-kid dyad	Parturition area
June	1	Early rearing	Large mother-kid flocks	Alpine pasture
July	2			
August	3	Weaning	smaler scattered matriarchial groups few contacts with males	Hot weather domestic flocks High altitude, summer home ranges rocks, shadow
September	4			
October	5	Rut	mixed flocks	large pasture
November	6			
December	7			
January	8		Median size mixed or matriarchial herds	Snow high altitude rocky cliffs and ridges
February	9			
March	10		Females-kids groups	
April	11		Large mixed flocks	Lower pasture with spring grass
May	12	Mother's isolation	Diversity of grouping	
June	13		Juvenile associations	
July	14		Yearling females join nurseries	Alpine pasture
August	15		Some yearling males join male groups	Former summer home ranges
September	16			
October	17		Mixed flocks	
November	18	Rut	Yearling females participate in rutting associations	Former pasture
December	18			
January	20		Mother-yearling daughter associations with or without males	Snow high altitude rocky cliffs and ridges
February	21			
March	22			
April	23		Large mixed flocks	
May	24	Possible parturition	Some yearling females became isolated	
June	25		Associations of young	Lower pasture with spring grass
July	26		Matriarchial associations with young	
August	27			Former summer home ranges
September	28			
October	29			
November	30	Rut	Mixed flocks	Former pasture
December	31			

status, as well as their great plasticity of grouping behaviour. Most of them rejoined nurseries of females with newborn kids during the summer. In June, half the yearling isards were observed in female-young groups in Ossau (Berducou and Bousses 1985), whilst 4/5 were observed in Orlu at the same time. This difference, as noted before for kids, can be related to the higher proportion of mixed groups in the Ossau population. It is possible that some of the yearlings may disperse, or follow adult males, as the young/female ratio did not recover the pre-parturition levels. Clutton-Brock et al. (1982) also reported, in red deer, a marked decline of mother-calf association during the new calving period, followed by an increase during the summer, which never reached the same level as that observed previously.

Young isard females are sexually mature and may already participate in reproduction in the second autumn of their life, as proved by a marked 2-year-old female observed nursing a kid in July. Table 2 shows a general view of the whole standard social trajectory with the various factors that might shape it.

On the one hand, social environment and, consequently, the social ontogenetic trajectory of an individual isard is, all along its path, submitted to external constraints. In our work as in many other studies, weather and snow-cover conditions were shown to have a great influence on the distribution of food and on the animal's pattern of habitat use (Petocz 1972; Hirth 1977; Lagory 1986; Bon et al. 1990). In this work as in others, the presence of very large prairies, for instance, proved to be responsible for large gatherings (Clutton-Brock et al. 1982; Schaal 1982; Maublanc et al. 1987). But all the external constraints that can occur are different, for a given species, amongst the various living areas, and even within the same area, between various home ranges. Furthermore, these environmental conditions are not similar from one year to another. Thus, the social environment of an individual isard appears to be fluid, and its own social experience is distinct from that of its conspecifics.

On the other hand, it is clear that biological events play a major role in shaping the individual social trajectories through various social environments. They are: a. experience before birth, through maternal stress for instance (Lott 1983), b. early mother imprinting (Lent 1974; Bouissou and Andrieu 1978; Berger 1979a; Lickliter and Heron 1984; Poindron et al. 1984), c. mating (Miura 1983), d. breeding (Bon et al. 1990), e. rearing young (Ferrari et al. 1988; Hillman 1987). The social context also shapes the trajectory through the relative proportion, density and social trajectories of the conspecifics (Berger 1979b; Clutton-Brock et al. 1982; Alados 1985). These factors act together to bring about a diversity of social environments that each individual will experience, that makes its actual social trajectory unique. The social structures are the complex pictures observed and they result from the network of interacting individuals, themselves influenced by the interacting factors mentioned. Social structures become constructed in the same way as the individuals during their ontogeny. Studying the interactions between individuals should contribute to a fuller understanding of the establishment of such a network, and the self-organisation mechanisms of animal associations (Richard-Hansen 1992b).

On another hand, only long-term studies on marked animals, like the one in progress in the Orlu population, will allow the general rules of the mechanisms underlying the self-construction of a social trajectory to be established.

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Zusammenfassung

Soziale Umwelt junger Gemsen (Rupicapra pyrenaica p.) aus den Pyrenäen während der Ontogenese

Die soziale Umwelt junger Gemsen *(Rupicapra pyrenaica p.)* aus den Pyrenäen wurde einige Monate lang untersucht, um die Entwicklung partieller sozialer Prozesse zu verfolgen. Wir nehmen an, daß das Sozialverhalten der Adulten zum großen Teil durch die Ontogenese bestimmt wird. Von 2001 Gruppen in offenen Bergregionen werden Alters- und Geschlechterverteilung beschrieben.

Während der Kindheit durchlaufen Gemsen beim Kontakt mit Artgenossen allgemein und innerhalb von Weibchengruppen im besonderen soziale Perioden. Beide Muster der Verbände können eine Rolle im Sozialisierungsprozeß spielen. Kitz-Bock-Kontakte erfolgen erstmals in der Brunstzeit und sind seltener. Die drastischsten Veränderungen in der sozialen Umwelt erfolgen in der nächsten Geburtsperiode. Im Frühjahr findet eine besonders sensible Sozialisierungsperiode statt, in der soziale Vereinigungen sehr wechselhaft sind und neue soziale Netzwerke entstehen. Die Rolle der Erfahrung der Ontogenese bei der Bildung sozialer Verbände wird diskutiert.

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Capture-recapture study of a population of the Mediterranean Pine vole (*Microtus duodecimcostatus*) in Southern France

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Abstract

Investigated the population dynamics of a *Microtus duodecimcostatus* population by capture-recapture in Southern France during two years. The study was carried out in an apple orchard every three months on a 1 ha area. Numbers varied between 100 and 400 (minimum in summer). Reproduction occurred over the year and was lowest in winter. Renewal of the population occurred mainly in autumn. The population contained erratic individuals which did not take part in the reproduction. Resident individuals had a longer life-span and home ranges always located at the same place. Mean adult body weight varied only among females in relation to the reproductive rate. The observed demography of *M. duodecimcostatus* could be explained by biological traits (litter size, longevity) and by features of the habitat (high and constant level of resources, low level of disturbance), suggesting that social behaviours are an important regulating factor of numbers.

Introduction

The Mediterranean pine vole (*Microtus duodecimcostatus* de Sélys-Longchamps) has a narrow geographic range: Portugal, Spain and Southern France (Niethammer 1982). Its population dynamics in natural habitats is unknown. The Mediterranean pine vole lives also in cultivated areas. Vineyards are very ancient in the Mediterranean Region (several centuries), and the Mediterranean pine vole is abundant in such a habitat though it causes no particular damage. But the culture of perennial plants (e.g. orchards) with summer irrigation transformed the Mediterranean pine vole's habitat in such a way that this rodent species has become a pest to agriculture for a few years (Guédon 1987, 1988). This indicates the potentialities of *Microtus duodecimcostatus* to colonize successfully particular habitats.

A research program conducted by several institutes (Association de Coordination Technique Agricole, Institut de la Recherche Agronomique, Service de la Protection des Végétaux) was started in 1986. The aim of this program is to study reproductive biology and population ecology of the Mediterranean pine vole and to develop an integrated struggle system (a risk foresight method and biological, chemical, physical, mechanical, and agricultural struggle methods based on a good knowledge of the species). We here present demographic data from a study focused on local population dynamics of *Microtus duodecimcostatus* in cultivated areas.

Material and methods

A capture-recapture study was started in 1989 in Southern France, in an arcea located 30 km east of Montpellier (43° 39′ N, 4° 11′ E). The region is an agroecosystem with intensive cultures distributed in many patches separated by thick boundaries made with shrubs, cypress or poplar. During two years we trapped a population in a 20-year-old apple orchard (Golden Delicious/E.M.9; pollinization is

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made by branches of other varieties). The main agricultural practices are: cutting and crunching of the branches in winter, regular weeding, chemical treatment by pulverization all along the cultural cycle, chemical manuring. The influence of the Mediterranean climate is partially masked because of summer watering. The main disturbance which occurred during the study was a plough partially breaking up the soil in winter 1989. No chemical treatment against the Mediterranean pine vole was carried out during our study. Presence of this vole is revealed, as this species digs up soil from the ground when it is burrowing.

The trapping procedure for subterranean rodents was developed by PASCAL (1984; PASCAL and MEYLAN 1986) for the fossorial form of the water vole (*Arvicola terrestris scherman*). This procedure was adapted for snap-trapping (GUÉDON and PASCAL 1992) and for live-trapping of the Mediterranean pine vole (present study). We used Longworth traps (baited with apple) the efficiency of which has previously been demonstrated (GUÉDON et al. 1990). Traps were distributed on a 1 ha area, along six parallel 5 m × 100 m strips divided into 25 m^2 squares (Fig. 1). Two trap-stations (when possible) were

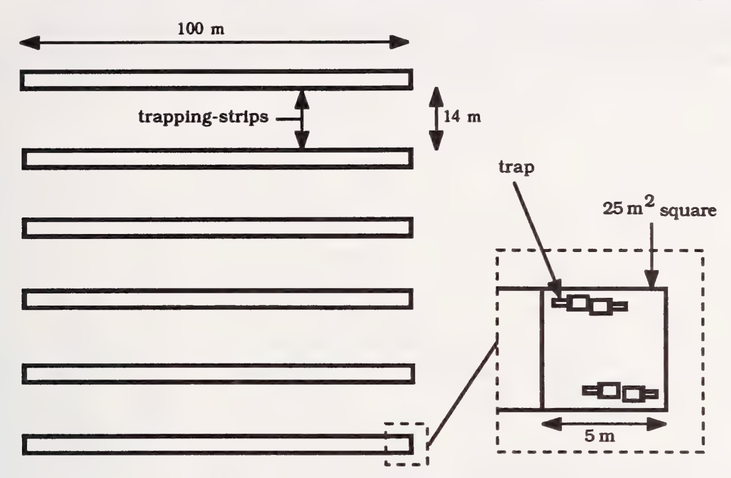


Fig. 1. Arrangement of the traps in the study area. In each square two, one, or no trap-station(s) were arranged in relation to the number of presence signs of Mediterranean pine vole on the ground. Each trap-station contained one, two or three traps

arranged in each square, each trap-station contained one, two or three traps orientated in the axis of the tunnel previously dug out. Each trap was open during 42 hours, and was checked 7 times. The caught animals were weighed (to the nearest g), marked by toe-clipping and ear-cutting, reproductive conditions (males: testes scrotal or abdominal, females: pregnant, lactating, and vulva open or closed) and coat color were noted before being released. It was also noted whether the trap was covered up with soil by the vole (named "trap-stuffing" by KREBS and BOONSTRA 1984), which is a typical behaviour of this species when its tunnels are opened. Two age-classes were distinguished according to weight, adult: > 17 g, and juvenile: ≤ 17 g. Strips were trapped two by two, so a trapping-session lasted 9 days. Trapping-sessions were carried out every 3 months.

Results

Demography

We caught 1,534 animals 4,656 times in 18,818 trap-checks. The observed numbers (Fig. 2) varied according to the seasons, with a decrease during summer droughts. Proportion of juveniles in the population was always low (Fig. 2). Sex ratio of the caught animals never differed from 1:1 (χ^2-tests), for adults as well as juveniles (Fig. 3, the greater fluctuations observed among the juveniles are caused by their smaller numbers compared with the adults).

Among the 429 individuals caught in February 1989, five were recaught in February 1991 (3 males and 2 females of which one was pregnant).

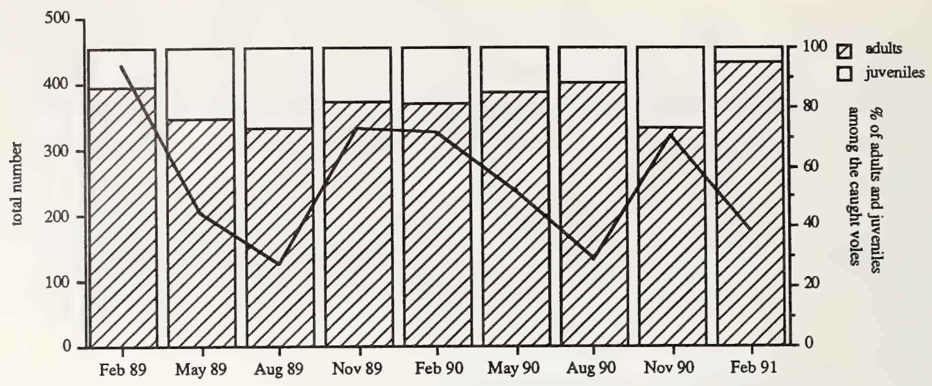


Fig. 2. Total number of caught voles (curve) and percentage of the two age-classes (histogram) during two years

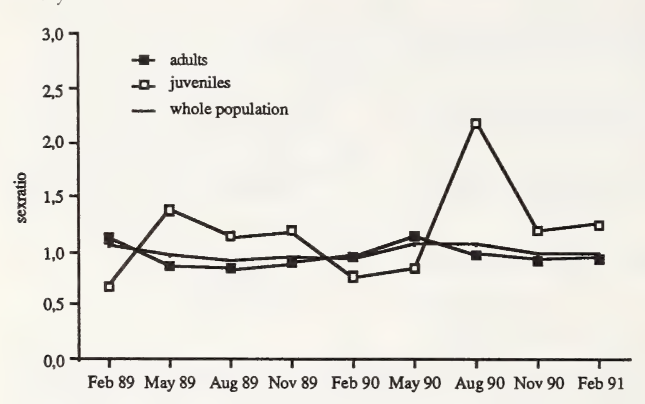


Fig. 3. Sex ratio of the juveniles (voles less than 18 g), the adults (voles heavier than 17 g), and all the voles caught (juveniles and adults)

Reproductive activity occurred over the year but showed seasonal variations. We exceptionally observed male individuals with scrotal testes, indicating that this position of testes is not a reliable sign for sexual activity in male *M. duodecimcostatus*. The proportion of females sexually active was at maximum in May, August and November, but seemed to show inter-annual variations (Fig. 4). This is corroborated by the proportion of juveniles

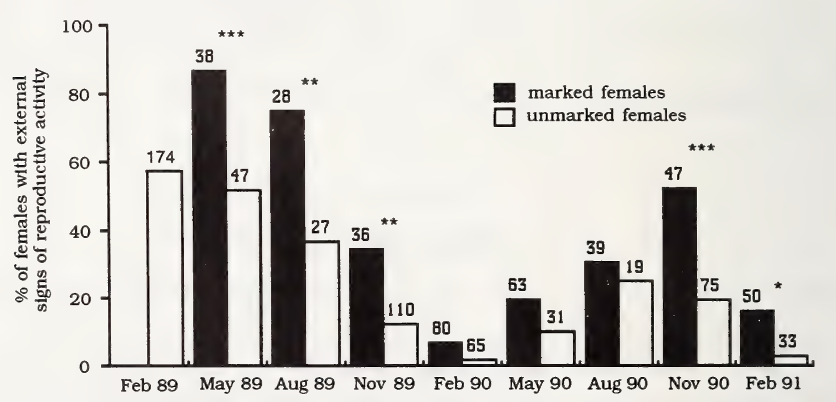


Fig. 4. The adult females caught during each trapping-session are divided into two categories: marked and unmarked (numbers of each category caught are indicated). The proportion of individuals with external signs of sexual activity for each category are plotted and compared (χ^2-tests, $^{*}0.01 < p < 0.05$; $^{**}0.001 < p < 0.01$; $^{***}p < 0.001$)

Table 1. **Mean body weight of the caught voles in each trapping-session**
(mean ± standard deviation)

session		Feb 89	May 89	Aug 89	Nov 89	Feb 90	May 90	Aug 90	Nov 90	Feb 91
adults	males	22.1 ± 2.2	21.8 ± 1.8	21.1 ± 1.9	21.1 ± 1.8	21.1 ± 1.7	20.7 ± 1.7	21.5 ± 1.7	21.0 ± 1.9	20.6 ± 1.4
	females	23.0 ± 2.8	23.3 ± 3.0	23.6 ± 1.8	22.4 ± 2.4	21.5 ± 2.1	22.0 ± 2.8	24.2 ± 1.6	21.8 ± 2.2	21.4 ± 2.3
juveniles	males	14.9 ± 2.2	14.9 ± 2.0	15.2 ± 2.1	13.4 ± 2.0	15.0 ± 2.0	14.8 ± 2.0	13.3 ± 2.3	14.4 ± 2.0	17.0 ± 0.0
	females	14.9 ± 2.3	14.2 ± 2.2	14.1 ± 2.4	15.3 ± 1.6	14.4 ± 2.3	14.4 ± 2.4	13.8 ± 1.9	14.7 ± 2.3	15.5 ± 2.6

in the population: maximum in August 1989 and in November the following year (Fig. 3). Captures of pregnant females which were lactating confirmed the existence of post-partum fecondation as was observed in the laboratory (Guédon et al. 1991a). The distinction between marked adult females (present for at least 3 months) and unmarked ones shows the following pattern: the proportion of females with external signs of reproductive activity was always higher among the former than among the latter (Fig. 4). This difference is not always statistically significant (χ^2-tests).

The variations in mean body weight of the caught voles did not show seasonality (Tab. 1). Mean adult body weight was slightly higher for females in contrast to males (range: 21.5–24.2, and 20.7–22.1, respectively), due to the presence of pregnant females. Standard deviation of adult body weight was slightly larger for females than for males (range: 1.6–3.0, and 1.4–2.2, respectively); this is probably due to the heterogeneity of pregnancy among the females (Fig. 4).

The proportion of unmarked animals (immigrants, animals born during the three previous months, or residents not previously caught: Fig. 5) varied with the seasons: it was at minimum in August and at maximum in November, indicating that renewal of the population occurred mainly in autumn.

Individual movements recorded during the study

Despite the low distance between two trapping-strips (20 m), the recapture rates from one strip to another were very low (0.4–16 %) indicating that, either movements of the Mediterranean pine vole were very restricted during the time of a trapping-session, or a decrease in the trappability of the voles occurred after a first capture. Analysis of movements between two trapping-sessions corroborates the former explanation: the majority of animals was recaught at the same place as they were caught three months before. Such sedentary animals were observed during several consecutive sessions: among 48 animals caught in four consecutive sessions, 38 (79 %) were always located at the same place. Home range locations seem constant over time, however, we cannot speculate on variations of home range sizes.

The proportion of animals caught twice or several times during the 7 checks (within trapping-session recapture rate) varied with the seasons (Fig. 6), suggesting a decrease in trappability during summer. This proportion was always higher for marked than unmarked animals (except August 1989).

Parameters related to the trapping procedure

Trapping-intensity varied slightly with the seasons: at minimum in August, and at maximum in November (Fig. 7). These variations were related to the lesser number of presence signs on the ground. Proportions of captures and of trap-

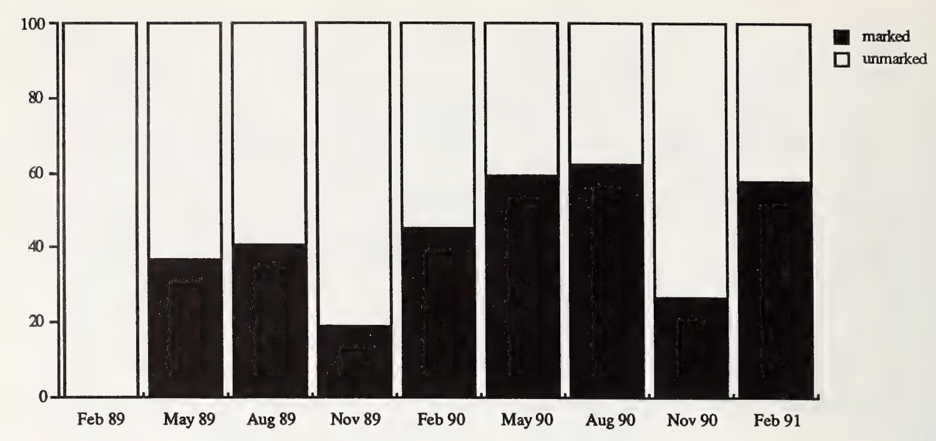


Fig. 5. Proportions of marked and unmarked voles caught in each trapping-session

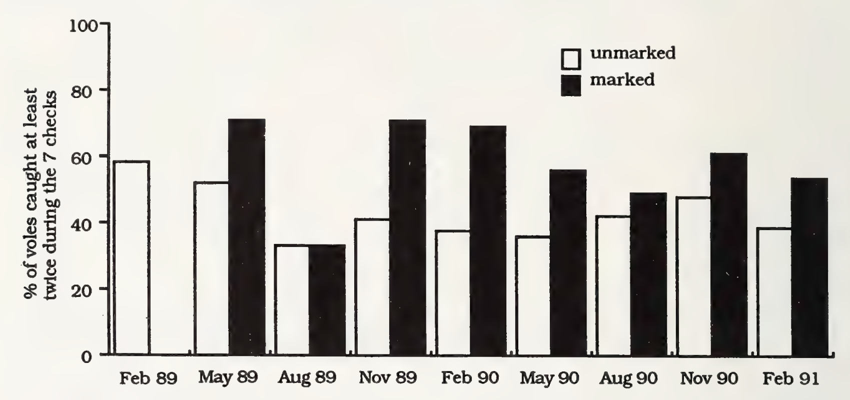


Fig. 6. Comparison of the proportion of voles caught at least twice during the 7 checks (within trapping-session recapture rate) between marked and unmarked voles

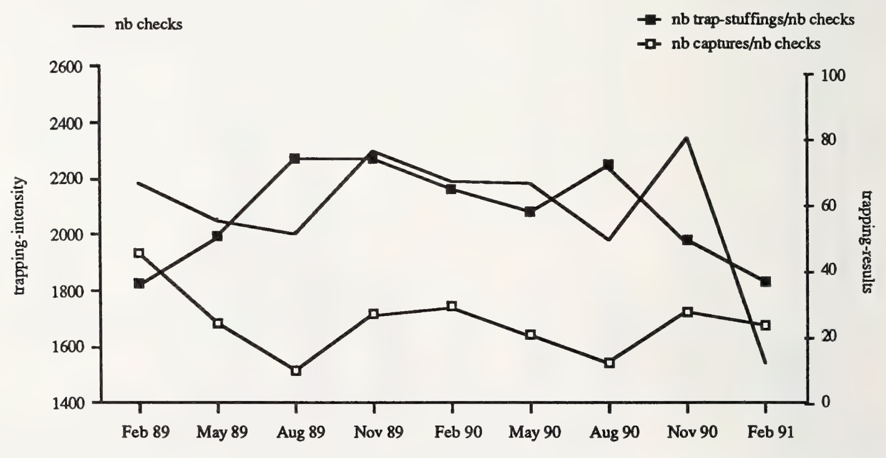


Fig. 7. Trapping-intensity (expressed as number of trap-checks: left axis) and trapping-results (number of captures and number of trap-stuffings reported to the number of checks: right axis) in each trapping-session

stuffings (reported on trapping-intensity) varied greatly with the seasons (Fig. 7). The proportion of captures was at minimum in August (= 10 %) and varied between 20 % and 45 % for the other sessions, the results of February 1989 (45 %) were not obtained again in 1990 and 1991. The proportion of trap-stuffings varied inversely with the proportion of captures.

Other species

Five other species were caught in our traps: *Crocidura russula, Apodemus sylvaticus, Mus musculus, Rattus norvegicus,* and *Mustela nivalis.* Numbers of captures for these species are indicated in Table 2. Herbivorous and granivorous small mammals were scarce in the underground habitat suggesting that competitive interactions with *M. duodecimcostatus* are

Table 2. **Numbers of captures for other species in the Longworth traps disposed in the underground habitat of *M. duodecimcostatus***

species	Feb 89	May 89	Aug 89	Nov 89	Feb 90	May 90	Aug 90	Nov 90	Feb 91
Crocidura russula								1	
Apodemus sylvaticus	8	6	2	1	2			2	1
Mus musculus								1	
Rattus norvegicus					1				
Mustela nivalis			1						

not important in our study area. Only one weasel (*Mustela nivalis*) was caught, indicating that predation by this species may not influence the population dynamics of the Mediterranean pine vole in our study area. A domestic cat (*Felis catus*) was observed in the orchard while hunting; however, raptor birds (*Strix aluco, Buteo buteo, Falco tinnunculus*) were regularly observed and were probably the main predators of the voles.

Discussion

Nearctic and Palearctic pine vole species are generally all included in the "*Pitymys* group" which is considered as a genus (Honacki et al. 1982; Corbet and Hill 1991) or as a subgenus included in the genus *Microtus* (Niethammer and Krapp 1982; Nowak and Paradiso 1983). Chaline et al. (1988) argued that the subgenus *Pitymys* is polyphyletic and proposed to divide it into the two subgenera; *Pitymys* (nearctic species) and *Terricola* (palearctic species). If Chaline et al. (1988) are right, it would implicate a converging evolution of some characters (particularly life-history traits as will be shown below) between *Pitymys* and *Terricola.*

In our population of *M. duodecimcostatus* we observed a decreased trappability during summer. The same phenomenon was observed in *M. pinetorum* (Lindquist et al. 1981; Cornbower and Kirkland 1983) and several *Microtus* species (Krebs and Boonstra 1984). Added to the fact that the proportion of trap-stuffings increased in summer, this leads us to invoke a more subterranean behaviour of the Mediterranean pine vole in order to avoid the hot and dry atmosphere. This changing behaviour may explain the decrease in captured voles during summer, however we cannot exclude a mortality peak during this season.

The age-classes chosen in our study were *ad hoc*: animals less than 18 g weighed more than 17 g three months later. A snap-trapping study demonstrated that some females less than 18 g could already be pregnant (Guédon unpubl. data). Body growth may be slower in nature than in captivity (Guédon et al. 1991b). However, the proportions of juveniles

were always low. This can be explained by a low trappability of this age-class: voles were not caught before they weigh at least 8 g. Mc Guire and Novak (1984) and Salvioni (1988) observed that behavioural development was slow in juveniles of other pine vole species (*M. pinetorum* and *M. subterraneus*, respectively). Several studies showed that the proportion of juveniles was always low in populations of *M. pinetorum* (Simpson et al. 1979; Lindquist et al. 1981; Cornbower and Kirkland 1983). Fecundity in pine vole species is low compared with other *Microtus* species or other microtine genera (Lefèvre 1966; Pelikán 1973; Schadler and Butterstein 1979; Salvioni 1986; Guédon et al. 1991a, see Innes 1978 or Keller 1985 for reviews), and may influence the age-structure of the population.

A long life-span was observed in other pine vole species (Le Louarn 1974; Cornbower and Kirkland 1983; Salvioni 1986), and seems to be a trait of these microtine species. Some studies suggested that populations of *M. pinetorum* present a high turn-over (Miller and Getz 1969; Staples and Terman 1977; Simpson et al. 1979). Such a pattern is also present in our study; however, preliminar statistical analysis revealed that this was an artifact: most of the unmarked individuals were erratics and were not subsequently recaught (Paradis 1990).

The fact that reproduction occurs over the year in *M. duodecimcostatus* was also observed in Spain (Claramunt 1976; Palomo et al. 1989), and in populations of *M. pinetorum* living in orchards (Simpson et al. 1979; Cornbower and Kirkland 1983), though this species lives in a cooler climate. Reproduction in our population was at minimum during winter. This result is not in agreement with Palomo et al.'s study (1989) who showed that reproduction decreased dramatically during summer. This result is supported by a small number of caught animals (210 individuals during 2 years and only 4 females in summer), however, and a monthly snap-trapping study in Southern France (more than 7,000 individuals caught during 5 years) showed that reproduction decreased in June and July but increased in August (Guédon and Pascal unpubl. data). Discrepancy in the results of the two approaches (snap-trapping and live-trapping) can be explained by the fact that pregnancy cannot be detected in alive voles before about 10 days, but it can be determined at a state of about 6 days in dead samples (Keller 1985). Cohen-Shlagman et al. (1984) observed a decreased reproductive activiy in summer in *Microtus guentheri*, another Mediterranean microtine species. The seasonal variations of reproduction observed in our population could be explained by high summer survival of resident individuals due to high level of resources in underground habitat of apple orchards. This hypothesis could be tested by studying seasonal variations of reproduction in uncultivated habitats.

In the studied habitat, food is abundant and uniformly distributed, therefore reproduction is probably conditioned by available space (possibility to construct a burrow). In a population with sustained high densities, space is probably a limiting factor for access to reproduction (at least for females). This assumption is strengthened by the fact that reproductive females are resident (present for at least three months). Social behaviours were evidenced to mediate access to reproduction in many species of mammals (Hendrichs 1983; Dunbar 1985; Armitage 1987). Such a phenomenon may play a role in the local population dynamics of *M. duodecimcostatus.*

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Zusammenfassung

Markierungsfangstudien an einer Population der Mittelmeer-Kleinwühlmaus (Microtus duodecimcostatus) in Südfrankreich

Eine Population der Mittelmeer-Kleinwühlmaus (*Microtus duodecimcostatus*) wurde in Südfrankreich über einen Zeitraum von 2 Jahren durch Fang, Markieren und Wiederfang untersucht. In Abständen von 3 Monaten wurden Fänge in einem Apfelgarten auf einer Fläche von 1 ha durchgeführt. Pro Fangtermin wurden 100 bis 400 Individuen gefangen, am wenigsten im Sommer. Die Reproduktion fand das ganze Jahr über statt, war aber im Winter am geringsten. Eine Erneuerung der Population fand insbesondere im Herbst statt. Einzelne Individuen nahmen nicht an der Fortpflanzung teil. Seßhafte Individuen hatten eine längere Lebensdauer und ihr Aktionsraum blieb sehr konstant. Das Durchschnittsgewicht variierte nur bei Weibchen in Abhängigkeit von der Reproduktionsrate. Die beobachtete Demographie von *M. duodecimcostatus* kann durch biologische (Wurfgröße, Lebensdauer) und ökologische Merkmale (hohes und regelmäßiges Nahrungsangebot, geringes Störungsniveau) erklärt werden und weist darauf hin, daß das Sozialverhalten ein wichtiger Regulationsfaktor für die Populationsgröße sein könnte.

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Evaluation of hare abundance allowed by their use of attraction points

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Abstract

Studied the space use by hares *(Lepus granatensis)* which was affected by wooden stakes placed in an open grassland at Doñana Biological Reserve (SW Spain). Densities of hare pellets on plots centered on the stakes were higher than on plots not centered on them. The use of stakes by hares seems to be related either to an anti-predator behaviour or to a social behaviour of ground marking. Neither the time nor spatial variation in hare abundance was related to food supply or to the herbaceous layer characteristics. Rather, the seasonal abundance of hares in the study area depended on the flooding patterns of adjacent plant communities. The use of stakes as an improved version of the pellet-count method is proposed. This modified method considerably reduces the sampling effort necessary to carry out realistic estimations of spatial and seasonal variations in the relative abundance of hares in open fields.

Introduction

The ecology and behaviour of hares of the South Iberian Peninsula (*Lepus granatensis* Rosenhauer) is practically unknown. Their taxonomic status and geographic distribution were described by Palacios and Meijide (1979) and Palacios (1983), but these aspects have recently been questioned (Schneider and Leipoldt 1983; Bonhomme et al. 1986; Corbet 1986; Palacios 1989). These animals live in habitats characterized by a high abundance and diversity of predators (Soriguer and Rogers 1979) that can strongly influence their activity pattern and space use.

Among other reasons for the lack of information about this species is the high time-and-monetary cost of the traditional methods for studying lagomorph abundance and its temporal and spatial variation: capture-recapture, road-side surveys and pellet counts (Taylor and Williams 1956; Burnham et al. 1980). These methods do not seem to be very suitable for low density populations because of the high sampling effort necessary to obtain realistic estimations.

An alleged behaviour of hares due to the presence of attraction points in an open grassland is described in this study. It allows the application of a new method to estimate spatial and temporal variations of their abundance in open fields at low population densities. Through its application the first information about the seasonal pattern of hare distribution at Doñana Biological Reserve (SW Spain) is given, as well as its relation to environmental variables.

Material and methods

Study area

The Doñana Biological Reserve (37°N, 6°W; SW Spain) is an area with Mediterranean climatic characteristics and a strong seasonality in the temperature and rainfall regimes. Two biotopes can be distinguished mainly within its 67 km^2: the salt marsh, and the scrubland on sandy soil (Rogers and Myers 1980). The salt marsh is flooded during the winter and spring months (November to May), and remains dry the remainder of the year. Its plant cover is mainly sedges (*Scirpus maritimus* and

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Eleocharis palustris), whereas the scrubland shows a high basal cover by browse species (mainly *Halimium* spp., *Stauracanthus genistoides*, and *Erica* spp.). An ecotone zone located between the scrubland and the salt marsh is occupied by communities of herbaceous plants with a floristic composition determined both by the depth of the water level and the soil salinity (Allier and Bresset 1978).

The work was carried out within a plant community of the ecotone zone. The study area is located on sandy-clay soil, between the salt marsh and a *Juncus maritimus* community. The ground is characterized by a complete lack of relief, and is usually flooded during the winter dependent on rainfall. The plant cover is very homogeneous and only small-size forbs and grasses are present. Some representative species are *Plantago coronopus, Aeluropus littoralis, Hordeum marinum, Polypogon maritimus* and *Frankenia laevis*. Plant nomenclature follows Valdés et al. (1987).

Pellet counts

In October 1989, 20 pairs of 1 m^2 plots were fixed in the study area. Each plot in a pair was 10 m away from the other one. Paired plots were numbered in sequence and placed every 20 m along a straight line perpendicular to the line delimited by the two plots in a pair (Fig. 1). A wooden stake, 16 cm^2 in square-section with its top 30 cm above the ground level was driven at the centre of the right plot of each pair (marked plot). The minimum distance between each stake and the nearest rush bed (JD) was measured with an accuracy of 1 m.

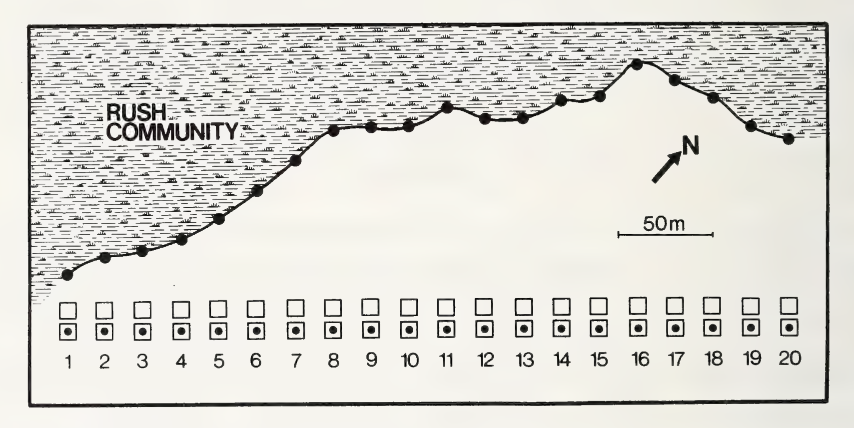


Fig. 1. Location of marked plots (squares filled with a point) and un-marked plots (white squares) in the study area. For clarity, plots appear larger than would be expected according to scale. Black points at the rush community edge do not represent its actual limits but the minimum distance from each stake to the nearest rush bed

From November 1989 to the beginning of March 1990 the study area remained flooded. Monthly pellet counts on the marked plots were carried out from March to September and in November. The number of pellets on each plot (PN) was counted and a mean density of pellets (MDP) was calculated for each month. In the June sampling all the pellets from the odd-numbered plots marked with stakes were removed. Thereafter until the end of July an intensive sampling was carried out (18 counts), the numbers of pellets appearing since the last count being recorded. The average time (± s.e.) elapsed between two consecutive counts was 3.59 ± 1.05 days. After each count the pellets were removed only from the odd-numbered plots. Additional pellet counts were carried out on the un-labelled plots in April, June, September and November.

Vegetation sampling

Estimates of the dry biomass availability (DB), the water content of vegetation (HC), the maximum height of green grass (MH), the basal cover of the herbaceous vegetation (SC), the forb contribution to the total cover (FC), and the contribution of dead grasses to the total basal cover of grasses (GC) were obtained monthly. The aerial biomass of the herbaceous layer was estimated on five 0.2 m^2 plots, fixed regularly along the straight line delimited by the stakes. The pasture samples were weighed with an accuracy of 0.1 g and dried in a hot-air oven at 50 °C until constant weight. The maximum height of

green grass was measured on each labelled plot with an accuracy of 1 cm. Cover estimates were carried out visually on each plot using an ordinal scale (WALKER 1976).

Some data were analysed using non-parametric statistical tests (SIEGEL 1956). A significance level of 0.05 was fixed for all analyses.

Results

Use of stakes

The differences between the mean density of pellets on both marked and unmarked plots were obvious during the entire study period (Tab. 1). Visual inspections of the un-labelled plots did not show different pasture characteristics with regard to the labelled plots, as expected by the short distance between them. Thus, the high number of pellets on the marked plots suggests that the stakes operated as attraction centres for hares.

Table 1. **Mean pellet densities ± s.e. for the marked and the non-marked plots**

Pellets were removed from the odd-numbered plots marked with stakes after the counts in June. Thus, only the even-numbered plot counts (n = 10) were used for estimating mean pellet density at the marked plots in September

	Marked	(n)	Un-Marked	(n)
Apr	4.80 ± 1.17	(20)	0	(20)
Jun	32.89 ± 4.10	(20)	1.25 ± 0.39	(20)
Sep	6.59 ± 1.32	(10)	0.80 ± 0.28	(20)
Nov	24.89 ± 3.33	(20)	0.15 ± 0.11	(20)

n = number of 1– m^2 quadrats

Time variation

The use of the stakes by hares during the study period shows a pronounced seasonal pattern (Fig. 2). In March the sampling was carried out when the area had recently emerged from the winter flood and no pellets were detected on the plots. The maximum pellet densities around the stakes were observed in May, June and July. During the more intensive sampling of the marked plots carried out in the second half of this period, an appearance rate of 0.15 pellets m^{-2} day^{-1} was recorded. From July to September an

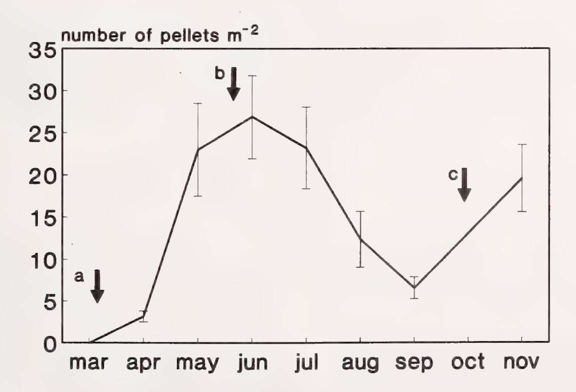


Fig. 2. Changes in the mean density of pellets ($\bar{x}$ ± s.e.) corresponding to the even-numbered plots of the transect line (n = 10). The arrows show: (a) the end of the flooding period at the study area, (b) the end of the flooding period in the marshland and (c) the beginning of autumn rains

important reduction in MDP was observed. In August and September the presence of hares at the study area was verified through the counting of new pellets appearing on the odd-numbered plots marked with stakes. Data for November showed a new increase in the mean density of pellets.

Lag-correlogram between the monthly values of MDP and the mean value of each vegetation variable (DB, HC, MH, SC, FC and GC), both estimated at the marked plots, showed no significant Spearman cross-correlation coefficient (P > 0.05 for all correlations).

Spatial variation

Spearman correlation coefficients (r_s) between PN and the vegetation variables estimated on each labelled plot (MH, SC, FC and GC) were calculated for each month. Due to the number of coefficients (28), by chance alone it could be expected that one would be significant under the no relationship hypothesis, and in fact, only one correlation between pasture characteristics and the number of pellets is significant (Tab. 2). However, a relation between the number of pellets and the distance from the stake to the nearest rush bed (JD) was indicated: the correlation coefficients are significant and positive for May, June and July and negative for November (Tab. 2).

Table 2. **Spearman correlation coefficients between the pellet number and the vegetation variables estimated on each plot of the marked transect line**

	n	MH	SC	FC	GC	JD
Apr	20	–0.074	0.064	–0.138	–0.338	0.102
May	20	0.235	0.384	0.355	–0.363	0.693**
Jun	20	–0.234	–0.122	0.325	–0.032	0.648**
Jul	10	–0.265	0.259	0.526	–0.540	0.748*
Aug	10	–0.345	–0.030	0.108	–0.075	0.480
Sep	10	0.348	–0.686*	0.166	–0.076	0.295
Nov	20	0.064	–0.061	–0.189	0.215	–0.620**

n = number of 1– m^2 quadrats; MH = maximum height of green grass; SC = basal cover of the herbaceous vegetation; FC = forb contribution to the total cover; GC = contribution of dead grasses to the total basal cover of grasses; JD = minimum distance between the stake and the rush bed. * $P < 0.05$; ** $P < 0.01$

The r_s between the number of new pellets appearing in the odd-labelled plots during the period of continuous sampling and JD showed a related probability very near the significance level (r_s = 0.642, P = 0.054, n = 10). No significant difference was detected between sampling distributions of the number of new pellets appearing in odd and even-numbered plots marked with stakes (K_d = 0.3, P = 0.99, n_1 = n_2 = 10, two-tailed test).

Discussion

Valverde (1960) and Kufner (1986) have pointed out that the salt marsh is the biotope of Doñana with the highest intensity of use by hares in summer and autumn. From November 1989 to June 1990 the salt marsh was flooded. During this period hares would have been forced to occupy the ecotonal areas between the marshland and the scrubland, as Valverde (1960) and Rau et al. (1992) suggest. As new areas emerged because of the decrease in the water level, the animals probably moved progressively into the salt marsh. This hypothesis would explain the absence of pellets in March, the slow increase detected subsequently in the mean density of pellets and their progressive decrease from June to

September. Early rains in October, usually responsible for the salt marsh flooding, could again cause the migration of hares towards the highest fields of the ecotone with the scrubland. This could be responsible for the increase in the mean pellet density recorded in November relative to the previous sampling in September. The observed seasonal pattern in hare abundance thus seems to be the result of a "concentration-dilution process" of hare numbers in the study area due to drastic reductions and increases of the available land surface.

The extent of the differences observed between the pellet counts in the marked and non-marked plots shows that stakes have operated as centres of attraction for hares. The accumulations of pellets around the stakes could reflect a ground-marking behaviour as well as an anti-predatory adaptation.

A social behaviour of ground marking through pellet grouping has been described for several lagomorph species. This behaviour is often manifested at points characterized either by their ground elevation or by the existence of easily identifiable landscape elements (Bell 1985). In the study area the stakes break the uniformity of a very homogeneous landscape and appear to be suitable points for the manifestation of such behaviour by hares. Pellet accumulations have been observed in brown hare (*Lepus europeaus* Pallas) ranges, but seem to be more related to the high levels of use of small areas than to the formation of latrines (Bell 1985).

On the other hand, the relevance for lagomorphs of vegetation cover as shelter against predation in Mediterranean environments has been pointed out by Jaksic and Soriguer (1981). In the study area diurnal and nocturnal predators of hares (e.g. Spanish imperial eagle *Aquila adalberti*, Iberian lynx *Lynx pardellus* and fox *Vulpes vulpes*) occur at very high densities (Kufner 1986). Therefore, in the absence of marked relief, high vegetation or relevant rocks, sufficiently large wooden stakes could provide hare shelter from predation. Perhaps the stakes break the hare figure, making it more difficult for predators to detect their prey and also could provide protective elements against direct attacks.

Both hypotheses can explain the significant and positive correlation observed for May, June and July between pellet numbers per plot and distance from the stake to the rush bed; they also explain the absence of a relationship between pellet numbers and the descriptive variables of the herbaceous layer at each labelled plot. Thus, stakes far away from the rush bed would be more attractive as reference elements for ground marking by pellet accumulations. On the other hand, during resting periods hares would use the stakes distant from the rush bed, situated in areas more exposed to predation, at higher frequency. The low use of the area before April and after the draining of the salt marsh can explain the absence of a relation between the pellet number and the distance to the rush bed for the sampling in April, August, and September. The ground level at the rush beds is elevated over the soil level at the plot locations. Thus, the November results could be interpreted in the sense of hares having to use the safe rush beds, and therefore the stakes adjacent to them, with regard to the flooding risk of the area after the first intense rain.

Hares do not show a conspicuous behaviour and commonly are solitary animals, although temporary grouping in feeding areas have been described for brown hare (Monaghan and Metcalfe 1985) and during the oestrus period for mountain hare *Lepus timidus* (Hewson and Hinge 1990). For that reason, estimations of their relative abundance with standard methodology are not usually feasible in areas occupied by low-density populations. Based on road-side surveys, time-and-spatial variations in hare abundance are very difficult to quantify because of the large number of visual contacts necessary to carry out the estimations (Burnham et al. 1980). Similarly, a large sample size is necessary, either in the number or size of plots, to obtain suitable data for estimating variations in abundance by the pellet count method (Taylor and Williams 1956). The results above suggest that the use of stakes could be a way to improve the pellet count technique reducing the sampling efforts for obtaining adequate sample sizes. This method has not

been tested at any other sites except at Doñana. However, this behaviour of hares is well known by Spanish hunters, who look for hares around land-marks and poles in open country. Also, personal observations by one of the authors, previous to the design of this study, at two other locations (Guadalquivir marshland and Cazorla Mountains, Southern Spain), suggest that this improved version of the pellet-count method could be widely used in open areas without high plant cover or relief. In such conditions a differential use of stakes would be expected to be due to variations in hare abundance.

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Zusammenfassung

Ermittlung der Abundanz von Hasen durch Nutzung von Anziehungspunkten

Die Raumnutzung des Iberischen Hasen *Lepus granatensis* in einem offenen Wiesengelände des Biologischen Reservates Doñana wurde experimentell durch eingebrachte Holzpfähle beeinflußt. Die Häufigkeit von Kotpillen war auf den Flächen größer, die mit Holzpfählen bestückt waren. Das Aufsuchen der Pfähle durch die Hasen steht wahrscheinlich im Zusammenhang mit Feindvermeidungs- oder Markierungsverhalten. Weder die zeitliche noch die räumliche Variation der Hasendichte ließ sich mit dem Futterangebot oder dem Kräuterspektrum korellieren. Dagegen scheinen Überschwemmungen die saisonale Dichte zu beeinflussen. Der Einsatz von Holzpfählen wird als Verbesserung der bisherigen Zählmethode vorgeschlagen. Er verringert deutlich den Aufwand, der nötig ist, um an zuverlässige Schätzungen der zeitlichen und räumlichen Schwankungen der relativen Dichte von Hasen im offenen Gelände zu gelangen.

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WISSENSCHAFTLICHE KURZMITTEILUNG

Unusual record of the Spotted hyena *(Crocuta crocuta)* in Rio Muni, Equatorial Guinea (Central Africa)

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The spotted hyena (*Crocuta crocuta* Erxleben, 1777) has a subSaharan distribution, spreading out over the savannah of Guinea and Sudan, showing preference for flat, open grassland areas, and avoiding the closed forest areas of the Congo basin (Kruuk 1972; Rosevear 1974; Kingdon 1977).

On the night of September 27 to 28, 1991, a strange specimen, even for local people, was killed by an automobile near Ndumu village (Nsork) on the south-eastern side of Rio Muni, Equatorial Guinea (1° 27′ N, 11° 10′ E). The animal, spotted and dog-like, was photographed before being dissected. The photographs and some recovered skeletal remains (tympanic bulla, left mandible together with its dentition, upper premolars, phalanxes and cervical vertebrae), were compared with the available material deposited in the collection of the Estación Biológica de Doñana, (Sevilla), which allowed us to identify the specimen as a spotted hyena *(Crocuta crocuta)* beyond any doubt. It has not been possible to determine its sex from the photographs because sexual dimorphism is very slight in this species and genitalia of both sexes appear very similar externally.

According to the third lower premolar wear, the specimen was a young adult, being included into Kruuk's age class III (between 3 and 6 years old) (Kruuk 1972). This agrees with the spot pattern of the skin, clearly defined all over the body. By counting the incremental lines in cementum of the decalcified and stained medium incisor, an age of seven years could be established for the individual, in accordance with the first estimation based on teeth wear, according to Van Jaarsveld et al. (1987).

The importance of this record lies in the fact that the spotted hyena killed in Equatorial Guinea was in a closed wet lowland forest, in the middle of the Congo basin forest block. The existence of a stable population of spotted hyena in Equatorial Guinea can be rejected because of the long distance from its known distribution area and because it would have been detected by us over a period of more than 5 years, living in this small country (26,000 km^2).

It seems more plausible that the record is related to an individual dispersal movement away from a distant population. Regarding the mobility of the spotted hyena, important displacements have been reported by Kruuk (1972) in Serengeti Park (Tanzania), related to the seasonal migrations of the large or medium-sized ungulates which they prey upon. In the Kalahari desert (Botswana), the spotted hyena wanders as far as 80 km a day (Eloff 1964). Occasionally, the spotted hyena occurs in gallery forests not far from grass-woodlands, following tracks or roads. This could be the explanation of a possible record in Ibadan, Nigeria, on the western limit of the equatorial forest block (Rosevear 1974). In these western populations, it is not unusual to see lone individuals (Happold 1987), a

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behavior possibly related to the diet and the distribution of food supply (KRUUK 1972; MILLS 1990).

The nearest appropriate savannah vegetation where the spotted hyena killed in Equatorial Guinea may have originated is located either in Cameroon or Gabon.

In fact, the nearest stable populations of *Crocuta crocuta* occur in Cameroon in Benoué and Boubandjidda Reserves (RONNEFELD 1969), but the species has not been seen south of 8°N. In Gabon, MALBRANT and MACLATCHY (1949) stated the farthest extension of the species to the north was N'Dende (4°S), at the southern boundary with the Republic of Congo. SMITHERS (1983) also reported its occurrence in the southern corner of the country, but apparently the spotted hyena has been exterminated from the savannah around Franceville. From either of these two possible points of origin, this spotted hyena specimen would have been faced with almost insurmountable hydrographic barriers (Sanaga, Ntem, Uoro, Ivindo, Ogooué rivers) on its way to Equatorial Guinea, more than 700 km distant in a straight line.

The present record of a spotted hyena in Equatorial Guinea, although exceptional, may not be the first. The existence of a specific name (Ocam-niat) in the Fang vernacular language, its presence in several popular tales and the different descriptions recorded among villagers by BASILIO (1962) as well as by ourselves, support this idea; its presence has also been mentioned by hunters in several localities in the Gabon forest. These displacements could be seen as evidence for deforestation or forest degradation on the edges of the Congo forest.

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We thank Mr. URCOLA and R. DELGADO for their assistance in field work, C. IBAÑEZ, M. DELIBES, C. KELLER, J. NEGRO and H. CASWELL for their helpful comments to the first draft of this manuscript. S. ZAPATA kindly made teeth preparations and counted the incremental dental lines. STEPHEN GARTLAN, WWF Representative for Cameroon, ALLARD BLOM, WWF Advisor, and some specialists gave us invaluable information. The work has partially been supported by the Spanish Instituto de Cooperación para el Desarrollo.

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Ausschreibung des Fritz-Frank-Preises
Förderpreis der Deutschen Gesellschaft für Säugetierkunde

Die Deutsche Gesellschaft für Säugetierkunde schreibt diesen Förderpreis in Höhe von DM 3000,– als Anerkennung für hervorragende wissenschaftliche Leistungen junger Forscher/innen aus.

Voraussetzung ist eine im Druck vorliegende Arbeit oder eine hervorragende Dissertation aus den Gebieten Phylogenie und Systematik, Verbreitung, Ethologie, Ökologie und Populationsbiologie der Säugetiere. Die Arbeit muß in den drei vorausgehenden Kalenderjahren erschienen oder als Dissertation begutachtet worden sein. Die Bewerber/innen dürfen beim Erscheinen der Arbeit bzw. bei ihrer Promotion nicht älter als 33 Jahre sein.

Bewerbungen der Vorschläge erbitten wir an die Geschäftsstelle der Gesellschaft, Prof. Dr. H. Erkert, Zoologisches Institut der Universität, Auf der Morgenstelle 28, D-7400 Tübingen, unter Beifügung von 5 Sonderdrucken bzw. Kopien der Dissertation bis zum 31. 3. 1993.

Der Jury gehören Wissenschaftler verschiedener Universitäten oder Museen und Mitglieder der Gesellschaft an.

Der Preis wird bei der Eröffnung der Jahresversammlung der Gesellschaft in Tübingen (26.–30. 9. 1993) überreicht.

Protokoll über die Mitgliederversammlung der Deutschen Gesellschaft für Säugetierkunde e. V. am 21. September 1992 im Vortragssaal in der Landesbibliothek Karlsruhe

Der 1. Vorsitzende, Herr Schmidt, eröffnet die Versammlung um 16.30 Uhr.

1. Die Tagesordnung wird angenommen.
2. Herr Schmidt verliest den Bericht über das abgelaufene Geschäftsjahr 1991. Im Berichtsjahr erschien der 56. Band der „Zeitschrift für Säugetierkunde“ in 6 Heften mit 384 Seiten. Zusätzlich wurde allen Mitgliedern das Sonderheft mit den Kurzfassungen der Vorträge und Posterbeiträge der Tagung in Hamburg zugesandt.
   Auf Einladung von Herrn Schliemann fand die 65. Hauptversammlung der Gesellschaft vom 22.–26. September 1991 in Hamburg statt. Themenschwerpunkte waren „Systematik und Stammesgeschichte der Säugetiere“, „Anpassung an aquatische Lebensräume“ und „Domestikation“. Erneut wurden herausragende Poster durch Buchprämien ausgezeichnet, welche die Verlagsbuchhandlung Paul Parey dankenswerterweise gestiftet hatte. Herr Schmidt dankte Herrn Schliemann und seinen Mitarbeitern für deren exzellente Organisation der Tagung.
   Die leichte Zunahme der Gesamtzahl der Mitglieder beruht auf Eintritten von Interessenten aus den neuen Bundesländern.
   Durch den Tod verlor die Gesellschaft folgende Mitglieder:
   Dr. K. Birkmann, Karlsruhe,
   Prof. Dr. J. Kratochvil, Brno,
   Prof. Dr. W. Schultz, Preetz,
   Prof. Dr. W. Vogel, München.
3. Herr Schmidt erläutert den durch Frau Kühnrich vorgelegten ausführlichen Jahresabschluß.
4. Die Kassenprüfer Bohlken und Schliemann haben keinen Anlaß zu Beanstandungen gefunden.

5. Die Anträge zur Entlastung des Schatzmeisters und des Vorstandes werden bei Enthaltung des Vorstandes angenommen.
6. Als Kassenprüfer für das Geschäftsjahr 1992 werden die Herren Bohlken und Schliemann wiedergewählt.
7. Der Vorstand sieht keine Veranlassung zur Veränderung des Mitgliedsbeitrages. Die Mitgliederversammlung stimmt zu, ihn bei DM 95,– für Vollmitglieder, DM 60,– für studentische Mitglieder und DM 10,– für Ehepartner von Vollmitgliedern zu belassen. Der Vorschlag, den Beitrag auf DM 45,– für Studenten aus den neuen Bundesländern zu ermäßigen, findet bei fünf Enthaltungen Zustimmung, nachdem Herr Dr. Georgi großzügigerweise zugesichert hat, daß der Verlag Paul Parey den derzeitg gültigen verbilligten Zeitschriftenbezug für diesen Kreis studentischer Mitglieder noch ein weiteres Jahr aufrechterhalten wird.
8. Die Mitglieder nehmen die Einladung von Herrn Maier an, die 67. Hauptversammlung vom 26.–30. September 1993 in Tübingen abzuhalten. Als Schwerpunktthemen werden „Offene Probleme der Phylogenie und Systematik der Großgruppen", „Geruchssinn und olfaktorische Kommunikation bei Säugern" und „Biologie der Primaten" gewählt. Die Einladung von Frau Spitzenberger, 1994 in Wien zu tagen, wird durch Akklamation angenommen.
9. Mit einer Gegenstimme und 16 Enthaltungen beschließt die Versammlung, daß die Gesellschaft Mitglied in der Union Deutscher Biologischer Fachverbände wird.
10. Herr Erkert begründet und erläutert die geplanten Satzungsänderungen und schlägt die Paragraphen einzeln zur Diskussion und Abstimmung vor. Mit Ausnahme von § 3, Satz 3 und § 18, Satz 3, die unverändert bleiben sollen, schließt sich die Mitgliederversammlung den Vorschlägen des Vorstandes mit der erforderlichen Mehrheit von über 75 % der Stimmen der anwesenden 73 Mitglieder an. Satz 2 von § 10 soll dahingehend präzisiert werden, daß der „jeweils presserechtlich verantwortliche Schriftleiter der Zeitschrift für Säugetierkunde" dem Vorstand angehören soll. Herr Schmidt gibt bekannt, daß der Vorstand eine Satzungskommission eingesetzt hat, die weitere konkrete Vorschläge für eine Modernisierung bzw. Aktualisierung der Satzung der DGS unter Einbeziehung von Vorschlägen der Reformkommission (TOP 11) erarbeiten und formulieren soll.
11. Herr Hutterer trägt die Vorschläge der Reformkommission vor, die anschließend von der Versammlung ausführlich diskutiert werden. Die Mitglieder werden aufgefordert, dem Vorstand bis zur nächsten Hauptversammlung Anregungen zu diesem Thema zukommen zu lassen. Die Mitglieder werden gebeten, sich in die Listen der zu gründenden Arbeitsgemeinschaften einzutragen. Bei fünf Enthaltungen billigen die Mitglieder den Beschluß des Vorstandes, DM 20 000,– auf ein Festgeldkonto zu übertragen und die Zinsen zu Förderzwecken zu verwenden.
12. a. Herr Schmidt würdigt nachdrücklich die Arbeit von Herrn Niethammer, dessen Gesundheitszustand unverändert geblieben ist.
    b. Er gibt die Einsetzung einer Tierschutz-Kommission unter dem Vorsitz von Frau Feddersen-Petersen bekannt und bittet die Mitglieder, sich mit Fragen, Vorschlägen und Anregungen zu dieser Thematik direkt an sie zu wenden.
    c. Herr Hutterer erklärt sich bereit, einen Fragebogen zu erarbeiten, der als Grundlage für eine Dokumentation über die Zentren der Säugetierforschung in Deutschland dienen soll.
    d. In der Zeitschrift für Säugetierkunde sollen pro Heft zwei Seiten für „Mitteilungen der Gesellschaft" zur Verfügung stehen. Frau Feddersen-Petersen sammelt Beiträge der Mitglieder und redigiert diese Mitteilungen.

Die Sitzung endet um 19.30 Uhr.

Prof. Dr. U. Schmidt	Prof. Dr. H. Erkert	Dr. H. Frädrich
1. Vorsitzender	Geschäftsführer	Schriftführer

Gaida, K.; Prokot, S.: **Microchiroptera.** Wien: Falter Verlag 1992. 144 pp., 48 Abb. 22 Farbtafeln. ISBN 3-85439-088-2

Das Büchlein enthält neun individuelle Beiträge über Fledermäuse in den Bereichen Zoologie, Ethnologie und Kunstgeschichte, Bildende Kunst, Literatur und Sinologie. Die Absicht der Herausgeber war es, die Spuren, die diese außergewöhnlichen Tiere in den verschiedenen Kulturkreisen hinterließen, in kurzen Übersichten darzustellen. Besonders eindrucksvoll gelang dies auch in dem Abschnitt „Sinologie der Fledermaus", vertreten doch gerade in diesem Kulturbereich die Fledermäuse in vielfältiger Form das Glück der Menschen. In weiteren Beiträgen wurden die Probleme der Echoortung, ihrer Evolution und schließlich die Besonderheiten des Fledermausfluges dargestellt. Die 22 verschiedenfarbigen, zum Teil kaum erkennbaren Sonagramme von Ortungslauten, lassen sich in der vorliegenden Form eigentlich nur unter der Rubrik „Bildende Kunst" einordnen.

E. Kulzer, Tübingen

Seifert, S. (Hrsg.): **Verhandlungsbericht 5. Internationales Symposium zur Erhaltung des Przewalskipferdes.** Leipzig: Zoologischer Garten Leipzig, Pfaffendorfer Straße 29, O-7010 Leipzig 1990. 343 S., zahlr. Abb. und Tab.

Wie man es bei Verhandlungsberichten häufig findet, ist auch in diesem Symposiumsband die Qualität der Beiträge sehr variabel. Das Spektrum reicht von mehr anekdotischen Beiträgen bis zu inhaltsreichen Darstellungen. Vier Hauptabschnitte (Komplexe) untergliedern den Band: I. Zucht und globaler Masterplan, II. Wiederauswilderung, III. Veterinärmedizinische, genetische und allgemeine Themen, IV. Anhang. 45 Einzelbeiträge werden entweder in deutscher, russischer oder englischer Sprache geboten. Insbesondere im Abschnitt über Wiederauswilderung finden sich die Informationen, welche in der ehemaligen Sowjetunion gewonnen wurden, nicht nur im russischen Original, sondern auch in einer deutschen Übersetzung.

Der erste Abschnitt beginnt mit der Übersetzung (Irmgard Schenk) eines historischen Dokuments aus dem Jahre 1881, der Beschreibung des Przewalskipferdes durch I. S. Poljakov. Anschließend bietet G. Krische eine historische Bilddokumentation (56 Abb.) zur Entwicklung der Zucht von Przewalskipferden. Für die Zucht der Art in Halle, welche durch die Lieferung eines Paares im Jahre 1901 begann, liefert L. Baumann eine mit 25 Abb. illustrierte Darstellung.

Von der im natürlichen Lebensraum höchstwahrscheinlich ausgestorbenen Art steht wieder eine Gefangenschaftspopulation von über 900 Tieren zu Verfügung. Diese schafft die Voraussetzung „für die Rückführung des Przewalskipferdes in seine angestammte Heimat" (S. Seifert). Insbesondere im Abschnitt Wiederauswilderung wird der Leser mit Problemen, welche sich bei diesem Vorhaben ergeben, konfrontiert. So wird geschildert, daß die Tiere in „Semireservaten" von der menschlichen Fürsorge relativ unabhängig werden sollen (Waltraut Zimmermann). Dort erhalten Junghengste die Möglichkeit, in Junggesellengruppen heranzuwachsen, in spielerischen Kämpfen ihre Kraft zu erproben um dann, 4- bis 5jährig, erfahren genug zu sein, sich in einem Harem durchsetzen zu können. Die Auswilderung muß unter streng kontrollierten Bedingungen erfolgen, wie W. E. Flint et al. in einem Beitrag darlegen. Es sind immer nur kleine Gruppen auszuwildern; schon in den Semireservaten sollten soziale Haremsgruppen gebildet worden sein, und zur genauen Überprüfung der Tiere muß gewährleistet sein, daß die Tiere vor der Freisetzung individuell markiert wurden. Es ist für die Kontrolle der Pferde vor und nach der Wiederauswilderung notwendig, daß bewährte und aufeinander abgestimmte tiermedizinische und genetische Verfahren angewandt werden. Diesen methodischen Gesichtspunkten sind die Kapitel im dritten Abschnitt des Bandes gewidmet, in dem auch von L. Schlawe das Problem der Nomenklatur domestizierter Arten in einem detailreichen Beitrag diskutiert wird. Mehr technische und organisatorische Probleme werden im Anhang behandelt.

Leider sind bei der redaktionellen Endkorrektur zahlreiche Druckfehler übersehen worden.

Der Herausgeber bezeichnet es in der Einleitung des Bandes als „Sternstunde . . . dabei zu sein und mitzuwirken, wenn eine Großtierart vor dem Aussterben bewahrt und der Natur zurückgegeben wird". Es ist zu hoffen, daß sich der in dieser Äußerung mitschwingende Optimismus bei der praktischen Arbeit bestätigt!

P. Langer, Gießen

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